THE AMMONITE FAUNAS AND STRATIGRAPHY OF THE UPPER PART OF THE UPPER KIMMERIDGE CLAY OF DORSET

by John C. W. Cope

ABSTRACT. Re-examination of 122·4 m of the Upper Kimmeridge Clay (Jurassic), from the Freshwater Steps Stone Band up to the Portland Sand of the type section, east of Kimmeridge, Dorset, has been undertaken, and bed-by-bed ammonite collections made throughout this thickness. The ammonites include representatives of three genera belonging to two subfamilies: twenty species and two subspecies are described. The following taxa are new: *Pectinatites* (*Pectinatites*) dorsetensis, P. (P.) strahani, P. (P.) circumligatus; Pavlovia composita, P. composita waddingtoni, P. superba; genus Virgatopavlovia, V. fittoni, V. hounstoutensis. The pallasioides Zone fauna is identified for the first time in Dorset, below the rotunda Zone, and a new zone, the fittoni Zone, introduced for the beds formerly correlated with the pallasioides Zone. Correlations are suggested with other areas of Britain and with the Volgian succession of Russia.

THIS paper follows on from earlier work (Cope 1967) on the ammonite faunas of the lower part of the Upper Kimmeridge Clay of Dorset, and includes material from the middle part of the *pectinatus* Zone up to the base of the Portland Sand. One horizon in these upper beds from which ammonites have long been well known is the Rotunda Nodule Bed; Sowerby figured his Ammonites rotundus from there and specimens from this horizon were subsequently figured by Neaverson and Buckman. Apart from in this horizon the ammonites are all crushed, often very indifferently preserved, and it is usually impossible to extract them intact from the rock. The development of a plaster-casting technique, and prolonged searching through the higher horizons have yielded hitherto undescribed faunas. Not surprisingly, the results shed light on the discontinuous record of Upper Kimmeridgian times further north in the southern English Midlands. The Hartwell Clay of Buckinghamshire has long been renowned for its beautifully preserved ammonites and provides the type area for the *pallasioides* Zone, the relative position of which was in dispute for nearly half a century. Only recently has this zone been correctly fitted into place by Casey (1967), and now for the first time it has been certainly identified in the type section of the Kimmeridge Clay and Casey's conclusion confirmed.

The collection made by Spath from these beds and housed in the British Museum (Natural History) (see Cope 1967, p. 5) contains little significant material from the horizons described here, but one of the Museum's collections which does contain very useful material is that made by C. H. Waddington in the 1930s; some of these specimens are figured and described below. The importance of the Waddington Collection lies in the fact that it contains large numbers of ammonites from the Rotunda Nodule Bed; this horizon has suffered very much from over-collection in recent years, and whilst Arkell (1933, p. 446) was able to talk of ammonites at this horizon 'standing out in hundreds', today it is very difficult to obtain any material at all.

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THE KIMMERIDGE SECTION

The uppermost beds of the Kimmeridge Clay are exposed in the area around Chapman's Pool. They are also seen further to the west, beyond the village of Kimmeridge, under the precipitous Gad Cliff, but there the section is somewhat difficult of access and, as it lies within the limits of an army firing range, may only be visited at infrequent intervals. The beds from which collections described here have been made is exposed from Freshwater Steps eastwards to the western side of St. Aldhelm's Head (text-fig. 1). The exposures, however, are discontinuous. From Freshwater Steps the gentle easterly dip brings successively higher horizons down to sea level. The first stretch of coast, the bay known as Egmont Bight, exposes the higher beds of the *pectinatus* Zone. The base of the succeeding *pallasioides* Zone reaches beach level at the eastern end of the bay. At this point it is possible, except after prolonged rain, to climb up the edge of the landslip with its large mud 'glacier' to examine the higher horizons right up to the Massive Bed (Arkell 1947a, p. 103), which marks the base of the Portland Sand, on the impressive western face of Hounstout Cliff. In the cliffs, however, the shale and mudstone are extensively weathered and the best collecting is on the ledges exposed at the base of the beach at low tide; here the rock is fresh and the fossils better preserved.



TEXT-FIG. 1. Section of cliffs from Freshwater Steps to St. Aldhelm's Head. Modified after Arkell 1933.

Beyond the 'mud glacier' is an extensive old landslip, well grassed over, in which are embedded large blocks of Portland Sand and Stone which are gradually washed out of the landslip by marine erosion and litter the beach. The *pallasioides* Zone reappears briefly in a low cliff beyond the landslip and is then cut off by another, probably older landslide. Eastwards again from this point is the semicircular bay of Chapman's Pool in which the *pallasioides* and overlying *rotunda* Zones are magnificently displayed. At beach level no further good exposure is seen to the east of Chapman's Pool because of extensive landslipping below Emmit Hill and St. Aldhelm's Head. There are intermittent small exposures up to the western end of St. Aldhelm's Head at beach level, but nowhere is it possible to locate the position of

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these occasional exposures stratigraphically with sufficient accuracy, because of their relative isolation and the lack of readily recognizable marker horizons in this part of the succession. However, a good section is visible above beach level below the steep-sided valley between Emmit Hill and St. Aldhelm's Head, known as Pier Bottom; this is obscured only by a little weathered shale debris and is free of vegetation. The exposure here is about 30 m above beach level and readily accessible from the coastal footpath. Some of the higher horizons may be studied here, but more extensive exposures of the upper beds can be seen on the western face of Hounstout Cliff. This can be approached from the coastal footpath on either side, or, as mentioned earlier, from beach level in the eastern corner of Egmont Bight.

The section has been remeasured using direct measurement throughout, and the thicknesses obtained corrected where necessary for any slope present. The result is that the total thickness from the Massive Bed down to the Freshwater Steps Stone Band differs only slightly from previous measurements by Blake (1875, 1880) and Arkell (1947a). However, thicknesses of individual beds, particularly in the upper part of the succession, vary considerably from earlier measurements. The system of bed numbering used is that of Blake since the beds are, for the most part, well defined and easily recognizable units. The Blake bed numbers were used by Arkell (1947a), and I also used his system for lower horizons of the Upper Kimmeridge Clay (Cope 1967). There are, however, two disadvantages of the Blake scheme. First, he included the top part of the Kimmeridge Clay in his Portland Beds scheme (Blake 1880), and secondly, he numbered his beds from the top downwards, a method which does not conform with modern practice. Blake's Bed 15 (1880) is readily recognizable as the Massive Bed (Arkell 1947a), the lowest horizon yet to yield Progalbanites, marking the base of the albani Zone, and thus the base of the Portlandian Stage. The Massive Bed is also taken as the local base of the Portland Beds. Blake's underlying bed (Bed 16 of the 1880 scheme) is not so well defined and seems to overlap with his Bed 1 of the earlier (1875) Kimmeridge Clav scheme. Below this horizon, however, each bed is readily identifiable, although for modern usage some of Blake's beds are too thick for precision, and can be lithologically subdivided. For this purpose I have used letters, but to follow the more usual practice I have lettered each bed from the base upwards—thus, for example, Bed 3a lies below 3b.

In the faunal lists given below the non-ammonite fauna has not been included. This is because it contains few species, though often these are quite abundant, and there is little variation throughout. *Liostrea multi-formis*, which readily encrusted the undersides of ammonites lower in the succession (Cope 1968b), is much less frequent than in lower horizons. Probably the only noteworthy form is *Rhynchonella* (*Rhynchonella*) *subvariabilis* which occurs, at times quite commonly, from the top of Bed 3 up to the top of Bed 1. The section below is listed from the top downwards.

Bed number Thickness (modified in after Blake) metres Virgatopavlovia fittoni Zone Hounstout Marl-variable pale and dark silty clays with three more sandy, 16c yellow-weathering, indurated bands near middle. Various partings visible within the thickness 21.00Virgatopavlovia hounstoutensis, V. sp. nov. aff. fittoni, Pavlovia spp. indet. Upper line of seepage on Hounstout. 16b Hounstout Clay-dark silty clays and mudstones, occasional more bituminous lavers 8.35 Virgatopavlovia fittoni, V. hounstoutensis, V. sp. nov. aff. fittoni, Pavlovia spp. indet. Lower line of seepage on Hounstout. 16a and 1d Rhynchonella and Lingula Beds (Upper part) - monotonous dark silty clays and mudstones 8.00 Virgatopavlovia fittoni, V. hounstoutensis, V. sp. nov. aff. fittoni, Pavlovia spp. indet.

Bed number (modified after Blake)		Thickness in metres
ujier bluke)	Pavlovia rotunda Zone	metres
16a and 1d	Rhynchonella and Lingula Beds (Lower part)—monotonous dark silty clays and mudstones, passing down into shales Paylovia spp. indet	15.00
1c	Rotunda Shales — shales and clays with layers of crushed white ammonites Paylovia rotunda, P. concinna, P. cf. concinna, P. spn. indet	13.50
lb	<i>Rotunda</i> Nodule Bed—hard calcareous nodules in clay. Nodules occur in at least two lines, the upper nodules often vertically elongated <i>Paylovia rotunda</i> . <i>P. rotunda gibbosa</i> . <i>P. concima</i>	1.80
la	Shales and clays	4.25
	Pavlovia rotunda, P. concinna, P. sp. B, P. spp. indet.	
2	Hard bituminous shales, middle part softer. Abundant ammonites. Forms pro- minent ledge to east of stream at Chapman's Pool and is conspicuous datum in cliffs to the west Pavlovia rotunda, P. conciuna, P. sp. nov. aff. raricostata, P. spp. indet	1.25
	Pavlovia pallasioides Zone	
3h	Shales and clays Pavlovia pallasioides, P. composita, P. composita waddingtoni, P. sp. B?, P. spp.	5.00
	indet., Pectinatites (Pectinatites) circumligatus.	
3g	Hard dicey clay Pavlovia pallasioides, P. superba, P. composita, P. composita waddingtoni, P. snp. indet	1.60
3f	Soft dicev clavs with occasional calcareous nodules	0.90
21	Paylovia pallasioides. P. superba, P. composita, P. spp. indet.	0 90
3e	Hard, grey, somewhat bituminous shales	0.40
	Pavlovia pallasioides, P. composita, P. spp. indet.	
3d	Soft dark-grey shales with thin (0.25 m) rusty-weathering harder band two-thirds	
	of way up	6.25
2	Pavlovia pallasioides, P. superba, P. composita, P. aff. strajevskyi, P. spp. indet.	0.60
3c	Prominent hard shale	0.60
36	Paviovia composita, P. sp. indet.	11.00
50	Pavlovia composita, P. sp. A, P. spp. indet., Pectinatites (Pectinatites) devillei, P. (P.) cf. devillei.	11.00
3a	Hard bituminous shale	0.30
4	Conchoidal fracturing clays with small nodules 0.9 m from base <i>Pavlovia</i> spp. indet. (mainly fragmentary and badly weathered in cliff).	4.00
	Pectinatites (Pectinatites) pectinatus Zone	
	Pectinatites (Pectinatites) pertinating Lone	
5	Bituminous shale	0.60
6d	Conchoidal fracturing clays, base hard and grey with slight seepage, more fissile	
	at top Pectinatites (Pectinatites) dorsetensis, P. (P.) strahani	4.00
6с	Clays with hard band at base Pectinatites (Pectinatites) strahani, P. (P.) dorsetensis, P. (P.) tricostulatus, P. spp. indet	1.50
6b	Clavs with two layers of small nodules	0.90
	Pectinatites spp. (abundant fragments throughout the bed).	
6a	Hard bituminous, rusty-weathering, shale <i>Pectinatites</i> spp. (fragments)	0.50

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(modified after Blake)	in metres
7 Clays with nodules 0.6 m and 1.8 m from top	4.60
Pectinatites (Pectinatites) dorsetensis, P. spp. indet.	
8 Hard shale (forms ledge over which waterfall drops at Freshwater Steps)	0.60
9 Shales	6.10
Pectinatites (Pectinatites) cf. pectinatus, P. (P.) cornutifer*, P. (P.) naso*. (P.) rarescens, P. (P.) paravirgatus*, P. spp. indet.	, <i>P</i> .
10 Freshwater Steps Stone Band	0.40
Pectinatites (Pectinatites) eastlecottensis Subzone below.	
Total thickness from base of Portland Sand	d 122.40

Species in Bed 9 marked with an asterisk were described by Cope (1967).

Fossil preservation and collecting technique

As with the lower part of the Upper Kimmeridge Clay, the ammonites of the upper part are crushed at virtually all horizons, and are unattractively preserved. For this reason they have been long ignored and it has been considered that they 'form hopeless material for investigation' (Neaverson 1925, p. 9) or that 'specific determination . . . is impossible owing to the bad state of preservation' (Arkell 1947*a*, p. 79). Uncrushed ammonites do occur in several of the calcareous nodule horizons, but apart from the well-known Rotunda Nodule Bed the nodules have not contributed to good preservation. The nodules are usually traversed by irregular calcite veins and the contained ammonites are invariably badly distorted and broken.

The vast majority of ammonites collected from the section are therefore crushed, and collection of these forms has in itself presented difficulties. The fissile nature of the rocks has resulted in fairly deep weathering in the cliffs, and it is only on the ledges exposed at low tide that collection of fresh material is at all possible. Unfortunately in some areas of the coast, shingle accumulations are usually high and it is only after severe storms that sufficient material is exposed free of shingle at the cliff base. From only one horizon within this succession, namely Bed 2, is the extraction of ammonites easy. Here in the relatively hard bituminous shales, the crushed ammonites usually separate readily from the matrix and may be lifted free of the shale. At some other horizons it is sometimes possible to extract the ammonites intact by removing a large portion of the rock with them. This is the case with the higher horizons on Hounstout Cliff.

Most of the ammonites have, however, been collected with a plaster-casting technique. This involves gently scraping away the exposed ammonite to leave a negative impression of its underside in the clay. This is then carefully cleaned and dental quality Plaster of Paris, thinly mixed, is poured on to the impression. After about twenty minutes it is possible to lift the plaster from the rock. The resultant cast is usually covered with a shell film from the original ammonite and thus presents perfectly adequate material for further work. Apart from the occasional presence of air bubbles these casts are often visually indistinguishable from the rushed ammonites. Preparation of the ammonites involves careful work to remove hard shale from the rib interspaces and the removal of pyrite aggregates. The specimens are treated after preparation with I.C.I. 'Bedacryl' which hardens the fragile shells and appears to prevent, or at least substantially delay, oxidation of the pyrite.

At all horizons, after ammonites have been collected, a considerable proportion are specifically unidentifiable even after complete preparation. At most horizons therefore, unidentifiable specimens form a significant part of the fauna collected. Since the ammonites are largely crushed, suture lines have almost invariably been completely destroyed and determination of the length of the body-chamber is determined by differential crushing of the shell. The sediment-free phragmocone is usually crushed slightly more than the sediment-filled body-chamber; with practice the point of change in the degree of crushing can be readily observed. Flattening of the ammonites has had a considerable effect on the original dimensions; the diameter of the shell and whorl height have been increased, the whorl thickness is a small fraction of the original dimension, whilst the umbilical diameter is probably little changed. In specific descriptions, therefore, when dealing with crushed material, the only dimensions quoted are the diameter and the umbilical diameter. The latter figure cannot be usefully quoted as a percentage of the shell diameter, as is conventionally done, since the crushed diameter is greater than the corresponding measurement in an uncrushed shell.

Rib density and style are the features that are of most use in determination and speciation of these

ammonites. In particular, rib density of the inner whorls seems to be a fairly constant character in most species, whereas outer-whorl ornament may vary considerably. No two specimens are the same in outerwhorl ornament, and while the numbers of primary ribs may in some cases be similar in different individuals of the same species, the numbers or arrangement of the secondary ribs, in the same individuals, may be very dissimilar. Such features as constrictions seem to be very variable and appear usually to be of little value in classification.





TEXT-FIG. 2. Rib styles in Upper Kimmeridgian ammonites.

SYSTEMATIC DESCRIPTIONS

Order AMMONITIDA Hyatt, 1889 Superfamily PERISPHINCTACEAE Steinmann, 1890 Family PERISPHINCTIDAE Steinmann, 1890 Subfamily VIRGATOSPHINCTINAE Spath, 1923 Genus PECTINATITES Buckman, 1922 Subgenus PECTINATITES Buckman, 1922

Type species (original designation). Ammonites pectinatus Phillips, 1871.

Diagnosis. As in Cope (1967, p. 59) except that the range of the subgenus is now extended upwards to include *pallasioides* Zone.

Remarks. In this subgenus I include all pectinatitids of the *paravirgatus* Subzone (and younger ones). As I indicated previously (1967, p. 20), Buckman's genus *Wheatleyites* is merely a *Pectinatites* with a particularly strongly ribbed bodychamber. *Paravirgatites* Buckman, 1922 and *Shotoverites* Buckman, 1925 are also typically pectinatitid on their inner whorls. The outer whorls are more coarsely ribbed and *Pavlovia*-like, and these forms may be considered intermediate between *Pectinatites* and *Pavlovia*. However, microconchs found associated with these latter forms have a ventral inflation, or a horn, so that they are better placed with *Pectinatites* than with *Pavlovia*. I earlier (1967, p. 63) associated one such species with the latter genus, but having now collected much more material from the higher beds of the *paravirgatus* Subzone, I include them not only in the genus, but the subgenus *Pectinatites*.

Pectinatites (Pectinatites) cornutifer (Buckman, 1925)

Plate 45, fig. 1; Plate 47, fig. 3

- 1925 Keratinites cornutifer Buckman, pl. 602.
- 1926 Keratinites nasutus Buckman, pl. 664.
- 1967 Pectinatites (Pectinatites) cornutifer (Buckman) Cope, p. 62, pl. 25, fig. 3; pl. 26, fig. 2.

Material. Two specimens (NMW 77.12G.5-6).

Stratigraphical range (amended from Cope 1967, p. 62). Upper Kimmeridgian, *pectinatus* Zone, upper part of *eastlecottensis* Subzone and lower part of *paravirgatus* Subzone, ranging from 6.0 m below to 4.6 m above Bed 10.

Description. Specimen 77.12G.5 is the more complete of the two; excluding the apertural horn, it is 105 mm in diameter, with an umbilical diameter of 33 mm. There are approximately fifty primary ribs on the last whorl, and rib density seems to compare well with the holotype of the species. It is more finely ribbed than the holotype of *P*. (*P*.) nasutus. Specimen 77.12G.6 also has about fifty ribs on its last whorl.

Ribs on inner whorls, very slender and markedly prorsiradiate; on outer whorl they swing forwards sharply from initial rursiradiate course, and are straight, prorsiradiate for remainder of length. Bifurcation low, secondary ribs quite closely paired. Constriction near peristome on specimen 77.12G.5, preceded by a virgatotome rib with four secondaries arising independently from anterior side of primary rib. Similar rib occurs one-quarter of a whorl back from peristome in holotype of *P. (P.) nasutus.* Horn 20 mm long, angled forwards on specimen 77.12G.5; on other specimen, horn missing, rest of peristome entire.

Remarks. The diameter of these specimens (each 105 mm) is greater than that previously recorded for the species, but in all other respects there is close agreement with the type material. Both come from 4.6 m above the Freshwater Steps Stone Band, which is higher than the species has hitherto been recorded.

Pectinatites (Pectinatites) cf. pectinatus (Phillips, 1871)

Plate 45, fig. 3

Material. One specimen (macroconch, NMW 77.12G.7).

Horizon. Bed 9, at 4.6 m above Bed 10. Upper Kimmeridgian, pectinatus Zone, paravirgatus Subzone.

Description. Estimated diameter 130 mm, with umbilical diameter of 58 mm. Estimated fifty primary and 105–115 secondary ribs on outer whorl. Only the last three-quarters of a whorl within the umbilicus is preserved; ribs there slender and markedly prorsiradiate, with low furcations. Outer whorl primary ribs much stronger, furcations predominantly polygyrate, but with simple and bifurcate ribs and intercalatory secondaries.

Uncoiling of umbilical seam over last half whorl suggests that the shell is probably mature. A crushed diameter of 130 mm is well within the size range of *Pectinatites* macroconchs; the specimen is thus probably fairly complete although no part of the peristome is preserved.

Remarks. This specimen shows quite close agreement in rib density with the specimen figured by Arkell and designated by him as the neotype (1956, p. 780, pl. 41, fig. 6). This latter specimen has fifty-seven primary ribs on the last whorl at a diameter of 115 mm; and at 90 mm diameter has sixty-four ribs. These figures are matched closely by the Dorset specimen, but since Arkell's specimen is incomplete it is not possible to match body-chamber ornament. It seems certain from the specimen, however, that it too is a macroconch.

This species is more coarsely ribbed than P. (P.) *eastlecottensis* Salfeld, 1913, which has about 139 ribs at 110 mm diameter, but is more finely ribbed and also considerably smaller than P. (P.) *dorsetensis* sp. nov.

Macroconchs of the subgenus *Pectinatites* are rare in the *paravirgatus* Subzone in Dorset, just as they are in the underlying *eastlecottensis* Subzone. My earlier view that P. (P.) *pectinatus* is the macroconch of P. (P.) *cornutifer* (Cope 1967, p. 62) is supported by the occurrence of the specimen described here at precisely the same horizon as that which yielded the specimens of P. (P.) *cornutifer* described above (p. 475). It would be necessary, however, to obtain better-preserved material of both forms, before drawing firm conclusions.

Pectinatites (Pectinatites) dorsetensis sp. nov.

Text-fig. 3

Diagnosis. Macroconch 210–285 mm in diameter; rib density as follows: at 30 mm diameter 39 ribs; 35 mm, 39–40; 40 mm, 40; 45 mm, 41–42; 50 mm, 41–42; 60 mm,

EXPLANATION OF PLATE 45

Fig. 1. *Pectinatites* (*Pectinatites*) *cornutifer* (Buckman). NMW 77.12G.5, ×1. Bed 9, 4.6 m above Freshwater Steps Stone Band.

Fig. 2. P. (\tilde{P}) circumligatus sp. nov. Holotype, NMW 77.12G.12, $\times 1$. Bed 3h, 3.65 m below Bed 2.

Fig. 3. P. (P.) cf. *pectinatus* (Phillips). NMW 77.12G.7, ×1. Bed 9, 4.6 m above Freshwater Steps Stone Band.



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42–43; 70 mm, 42–45; 80 mm, 42–46; 90 mm, 42–45; 100 mm, 41–42. Ribs of inner whorls rectiradiate to prorsiradiate, more widely spaced on outer whorl. Body-chamber with occasional simple ribs and intercalatory secondaries; polygyrate ribs common on some specimens.

Holotype, NMW 77.12G.13. Paratypes, NMW 77.12G.3, 4, 14, 15, 17-20.

Horizon. Holotype from top of Bed 6, 18.2 m above Freshwater Steps Stone Band.

Stratigraphical range. Upper Kimmeridgian, *pectinatus* Zone, *paravirgatus* Subzone, ranging from 11.0 m to 18.2 m above Freshwater Steps Stone Band (Beds 7-6d).

Description. All the specimens are too poorly preserved for the measurement of rib densities at diameters below 30 mm. For densities at greater diameters see Diagnosis (above). The ribs are of typical pectinatitid style on the inner whorls. On the outer whorl primary ribs become stronger and more widely spaced, with the furcation lower and with irregular development of secondary ribs. Polygyrate furcations occur commonly on some specimens, but are rare on the holotype and some others. Both simple unbranched primary ribs and intercalatory secondary ribs occur. The body-chamber is one-half to three-quarters of a whorl in length (measurement based entirely on the differential crushing of the outer whorl). Peristome simple and straight to somewhat sinuous, inclined forwards towards the venter. The umbilical seam uncoils over the last quarter to half whorl.

Remarks. This species is readily distinguishable from Pectinatites (Pectinatites) pringlei (Buckman) by virtue of its more finely ribbed outer whorl. The inner whorls, as far as it is possible to compare them, have a similar rib style to that species, as they do also to P. (P.) paravirgatus (Buckman), which has an even more coarsely ribbed body-chamber. Both these other species, however, are probably a little older than the Dorset forms, and the holotype of P. (P.) pringlei may have come from the basal part of the pectinatus Zone (Buckman 1925, legend to pl. 562), now distinguished as the *eastlecottensis* Subzone (Cope 1974*a*, p. 35). Certainly no specimen with fewer than thirty-eight ribs on the last whorl has been found in Dorset within the range of P. (P.) dorsetensis. This compares with thirty-two primary ribs on the last whorl of the holotype of P. (P.) pringlei. The other specimens of P. (P.) pringlei subsequently figured by Buckman (1926, pls. 562A, 562B) may belong to that species, but the specimen figured in plate 562A might equally belong to P. (P.) dorsetensis. It is not sufficiently complete for definite identification, but does come from a higher horizon than the holotype of P. (P.) pringlei. Paravirgatites pringlei Pruvost, 1925 is not related to the specimens figured by Buckman; it is a Virgatosphinctoides of the wheatlevensis Zone, similar to some forms from the wheatlevensis Subzone of Britain.

In style and arrangement the ribs of the outer whorl of *Pectinatites* (*Pectinatites*) dorsetensis resemble those of the outer whorls of pavloviids from higher horizons; this species is a good example of a form transitional from *Pectinatites* to *Pavlovia* and shows some characters of each genus.

Pectinatites (Pectinatites) strahani sp. nov.

Plate 46, figs. 1, 4

Diagnosis. Microconch *Pectinatites*, close to *Pavlovia* in outer whorl ribbing; inner whorls *Pectinatites*-like. Diameter 94-102 mm with following approximate rib densities: at 15 mm, 25 ribs; 29 mm, 25-29; 25 mm, 25-30; 30 mm, 26-30; 35 mm, 27.



TEXT-FIG. 3. Pectinatites (Pectinatites) dorsetensis sp. nov. Holotype, NMW 77.12G.13, Bed 6d. $\times 0.6$.

Ribs rectiradiate to prorsiradiate, fairly straight, heavier on body-chamber. Aperture inflated anteriorly or with feeble horn.

Holotype, NMW 77.12G.10. Paratypes, NMW 77.12G.1, 2, 11.

Horizon. Holotype from Bed 6 at 1.8 m above Bed 7. Paratypes from 13.2 m above Bed 10 (Bed 6 at 1.9 m above Bed 7).

Stratigraphical range. Upper Kimmeridgian, *pectinatus* Zone, *paravirgatus* Subzone, ranging from 13·10 m to 14·55 m above Freshwater Steps Stone Band (Beds 6c and 6d).

Description. The holotype is 94 mm in diameter with an umbilical diameter of 35 mm. Estimated twentynine primary and fifty-two secondary ribs on last whorl. For rib densities see Diagnosis (above). Ribs initially rursiradiate but swing forwards sharply at umbilical shoulder to become rectiradiate or prorsiradiate for remainder of their length. Furcation point variable, some furcations visible on innermost whorls.

Outer whorl ribs stronger, more blunt in cross-section, gradually more widely spaced. One or two constrictions on outer whorl of holotype to judge from close approximation of two pairs of ribs, but preservation does not allow this to be ascertained. At least one polygyrate rib on outer whorl of holotype and several simple ribs. The body-chamber appears, from differences in crushing, to be fractionally over half a whorl long; uncoiling of umbilical seam over this part of shell. Peristome on holotype is simple, possibly a little inflated anteriorly. Paratype 77.12G.2 has aperture which bears a horn, but this only projects ventrally by about 3 mm. This feeble development of the horn contrasts greatly with *P. (P.) cornutifer* (Buckman) in which the horn may project as much as 39 mm (Cope 1967, p. 62, pl. 25, fig. 3). The small horn is similar to that of some of the earlier species of *Pectinatites* (see Cope 1967 for illustrations) and is a mid-way point morphologically (and phylogenetically?) between the subgenus *Pectinatites*, and *Pavlovia* where the microconchs have straight peristomes. There is a marked constriction behind the peristomal region in paratype 77.12G.2, and between the constriction and the peristomal border itself ornament is subdued.

Remarks. This species is apparently intermediate between *Pectinatites* and *Pavlovia*. The feeble development of an apertural horn could, perhaps, be considered a valid reason for not including it in *Pectinatites*. The rib style of the inner whorls is, however, more typical of *Pectinatites*, in particular the initial rursiradiate course of the ribs followed by a sweep forwards at the umbilical shoulder. The pattern of rib densities is also more like that of *Pectinatites*; the figures for the numbers of ribs are seen to increase with diameter in this species. This is usual in *Pectinatites*, but unrecorded in *Pavlovia* at small diameters, where quite frequently there is a sharp decrease in the number of ribs. Comparison of this species with other species of the subgenus *Pectinatites* shows that the main differences lie in the fact that this species is more coarsely and stoutly ribbed. This stouter ribbing is also characteristic of the subgenus *Arkellites* (Cope 1967) which has not, however, been recorded above the basal part of the *eastlecottensis* Subzone; this latter subgenus is normally horned. For these reasons I include the species in the subgenus *Pectinatites*.

From the horizons at which this species has so far been recorded, the macroconch species P. (P.) dorsetensis sp. nov. occurs. It is thus possible that P. (P.) strahani is

EXPLANATION OF PLATE 46

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Fig. 1. Pectinatites (Pectinatites) strahani sp. nov. Paratype, NMW 77.12G.2, ×1. Bed 6c, 1.8 m above Bed 7.

Fig. 2. *P*. (*P*.) *devillei* (de Loriol). NMW 77.12G.8, ×1. Bed 3b, 1.8 m above Bed 4.

Fig. 3. P. (P.) cf. devillei (de Loriol). NMW 77.12G.9, ×1. Bed 3b, 10.0 m above Bed 4.

Fig. 4. P. (P.) strahani sp. nov. Holotype, NMW 77.12G.10, ×1. Bed 6c, 1.9 m above Bed 7.



COPE, Kimmeridge Clay ammonites

the microconch of that species, though rib-density considerations argue strongly against the association of the two forms.

Pectinatites (Pectinatites) tricostulatus (Buckman, 1923)

Text-fig. 4

1923 Wheatleyites tricostulatus Buckman, pl. 365.

1947b Pectinatites tricostulatus (Buckman) Arkell, p. 108.

1957 Wheatleyites tricostulatus (Buckman); Arkell, p. L330.

Material. One specimen (NMW 77.12G.16).

Horizon. Bed 6c, 14.2 m above Freshwater Steps Stone Band. Upper Kimmeridgian, pectinatus Zone, paravirgatus Subzone.

Description. Specimen fairly complete to a crushed diameter of 300 mm; beyond this shell broken, distorted, part clearly missing; complete shell had crushed diameter of at least 380 mm. The holotype is 235 mm in diameter; Buckman (1923) estimated maximum diameter about 415 mm. This corresponds to a crushed diameter only slightly more, as the holotype has a partially crushed outer whorl.

The umbilical diameter is 40% of the diameter (a figure comparing very closely with the holotype). The last part of the body-chamber is broken along the umbilical seam in the specimen figured here, thus giving initially a misleading impression of the umbilical diameter on that part of the shell.

Ribs of inner whorls slender, sweeping forwards to become prorsiradiate at umbilical shoulder, then fairly straight for remainder of visible length. Inner whorls ill-preserved, but about fifty-two ribs at diameter of 80 mm. The holotype has similar rib density at this diameter. Outer whorl ribs suddenly more widely spaced, and instead of regularly bifurcating become polygyrate in main with three secondary ribs to each primary. In addition, there are simple primary ribs and intercalatory secondaries. On the latter part of the (preserved) whorl the ribs, especially the secondaries, begin to fade.

Traces of umbilical seam preserved beyond present mouth of the shell suggest almost one-quarter of a whorl missing from this specimen; the body-chamber appears, from differences in degree of crushing and the umbilical seam trace, to be fractionally over half a whorl long.

Remarks. This single specimen compares very closely with the holotype and there can be no doubt that the two forms are conspecific. *P.* (*P.*) opulentus (Buckman, 1923, pl. 383A (only)) differs in having a more accelerated development of styles of ornament than *P.* (*P.*) tricostulatus. The development of coarse ornament appears earlier, and polygyrate secondary ribs appear at least as far back as the last umbilical whorl in the former species. This trend is even more developed in *P.* (*P.*) rarescens (Buckman, 1925, pls. 561A, 561B) where the secondary ribs have faded completely on the body-chamber (see below p. 485). Buckman's records suggest that the holotypes of all three species came from the same horizon at Wheatley (the Wheatley Sands of Buckman, later renamed the Pectinatus Sandstone (Arkell 1947b, p. 108)), but the Dorset succession shows that *P.* (*P.*) tricostulatus and *P.* (*P.*) rarescens, although from the same subzone, are not from precisely the same horizon. If, as seems possible, there

EXPLANATION OF PLATE 47

Fig. 1. *Pavlovia concinna* (Neaverson). NMW 77.12G.53, ×1. Bed 2. Small, incomplete example showing typical inner whorl development of forms in Bed 2.

Fig. 2. *P. rotunda* (Sowerby). NMW 77.12G.121, ×1. Bed 1, 1.8 m above Bed 2. Typical crushed form from shales below Rotunda Nodule Bed.

Fig. 3. *Pectinatites (Pectinatites) cornutifer* (Buckman). NMW 77.12G.6, ×1. Bed 9, 4.6 m above Freshwater Steps Stone Band.



COPE, Kimmeridge Clay ammonites



TEXT-FIG. 4. Pectinatites (Pectinatites) tricostulatus (Buckman). NMW 77.12G.16, Bed 6c. ×0.43.

is an evolutionary trend in this species group for rib styles to persist longer, then P. (P.) opulentus might be expected somewhere between the horizons of the other two species. The fact that all the species are recorded from the same bed in the Oxfordshire area is not surprising, since it is now well established that the successions in that region are highly condensed.

Pectinatites (Pectinatites) rarescens (Buckman, 1925)

Text-fig. 5

1925 *Wheatleyites rarescens* Buckman, pls. 561A, 561B. 1947*b Pectinatites rarescens* (Buckman) Arkell, p. 108.

Material. One specimen, photographed in situ. Not collected.

Horizon. 1.8 m above Freshwater Steps Stone Band. Upper Kimmeridgian, pectinatus Zone, parvirgatus Subzone.

Description. The specimen figured here was photographed *in situ* by the writer in 1969. It was 493 mm in diameter and had an umbilical diameter of 230 mm. Innermost whorls visible show ribs are already quite widely spaced. Outer whorl has only twenty primary ribs and no secondary ribs are visible on the last three-quarters of this whorl. The (presumed) peristome is simple, and the body-chamber appears to be just under half a whorl in length.

Remarks. The holotype (Buckman 1925) shows a rib style very similar to the phragmoconic part of the Dorset specimen; the paratype, on the other hand, is very similar in body-chamber ornament to the specimen figured here. With a maximum diameter of 480 mm this latter specimen compares well with the Dorset form when increase in diameter due to crushing is taken into account.

The relationship of *P*. (*P*.) rarescens to other species is discussed fully above (p. 482).

Pectinatites (Pectinatites) devillei (de Loriol, 1874)

Plate 46, fig. 2

- 1874 Ammonites devillei de Loriol, p. 270, pl. 1, figs. 13, 14.
- 1924 Ammonites devillei de Loriol; Ilovaisky, p. 343.
- 1936 Pectinatites (Keratinites) devillei (de Loriol) Spath, p. 23.
- 1956 Keratinites devillei (de Loriol) Arkell, p. 42.

Material. One specimen (NMW 77.12G.8).

Horizon. Bed 3b at 1.8 m above Bed 4. Upper Kimmeridgian, basal pallasioides Zone.

Description. The specimen is 66 mm in diameter with an umbilical diameter of 25 mm; approximately thirty-seven primary and seventy secondary ribs on last whorl. Inner whorls ill-preserved, ribs slender and crowded, projected forwards; furcation fairly high on whorl side compared with some other species of *Pectinatites*, as apart from on the last part of the umbilical whorls (which is affected by the uncoiling of the umbilical seam) the point of furcation of the ribs is barely visible.

Outer whorl ribbing becomes gradually stronger, more widely spaced. Body-chamber just over half a whorl long; this length is very readily determinable from the specimen, as the clay infilling of the bodychamber is exposed throughout its length and only a clay internal mould remains. Thus the strength of the ribs on the body-chamber displayed by the specimen is less than would have been the case had the shell been preserved there. Ventral part of the peristomal region well preserved; aperture bears a horn directed obliquely forwards. Horn distinctly ribbed, about 14 mm long (precise length is hard to ascertain as horn arises gently from ventral region). Ventral projection of horn about 10 mm.

Remarks. The specimen compares closely in all respects with de Loriol's (1874) figure of the holotype and with his full description. His uncrushed specimen had a diameter of 58 mm, which would be closely comparable with the Dorset specimen were it uncrushed. The rib density of the outer whorl (the only whorl visible on the Boulonnais specimen) is very similar to that of the specimen described here. The umbilical diameter of the holotype is slightly less than that of the Dorset specimen.



TEXT-FIG. 5. Pectinatites (Pectinatites) rarescens (Buckman). Photographed in situ in Bed 9, 1.8 m above Freshwater Steps Stone Band. $\times 0.34$.

The stratigraphical position of *P. devillei* in the British succession has long been in doubt. Before Buckman figured horned microconch pectinatitids from the south Midlands (*Keratinites* Buckman, 1925), all the microconchs of *Pectinatites* in old collections had been named '*Ammonites devillei*'—this being the only described horned pectinatitid. Buckman placed his *devillei* hemera above the *pectinatus* and below the *paravirgatus* hemera, though he did not figure or describe any specimen of *P. devillei*. Spath (1936, p. 153) stated that he had been unable to find *P. devillei* below the lowest crushed pavloviids in Dorset. It now appears that Spath was expecting to find this species too low in the succession, and that *P. devillei* lived alongside the early *Pavlovia* faunas in the *pallasioides* Zone. This is supported by their coexistence in the Boulonnais, albeit in a condensed succession there.

The Greenland specimen figured by Spath as *Pectinatites* (K.) aff. *devillei* (1936, p. 23, pl. 7, fig. 2a-b) lacks its peristome but does appear from rib style to be a microconch pectinatitid. However, the specimen came from the *pectinatus* Zone of Greenland and may thus well belong to an earlier species of *Pectinatites*.

No well-preserved macroconchs of *Pectinatites* have been found at this level in Dorset and the attribution of the form figured here to the subgenus *Pectinatites* is made in the absence of any knowledge of the macroconch.

Pectinatites (Pectinatites) cf. *devillei* (de Loriol, 1874)

Plate 46, fig. 3

Material. One specimen (NMW 77.12G.9).

Horizon. Bed 3b at 16.0 m below Bed 2. Upper Kimmeridgian, pallasioides Zone.

Description. The specimen is 70 mm in diameter with an umbilical diameter (somewhat distorted by crushing) of 28 mm. Approximately thirty-two primary ribs on last whorl. Inner whorls poorly preserved and it is not possible to determine rib density. Ribs slender, sweep forwards from umbilical shoulder, to which point there is an initial rursiradiate trend. From umbilical shoulder ribs rectiradiate to prorsiradiate; fairly low furcation visible within the umbilicus, secondary ribs closely paired. Ribs on outer whorl of similar style to those of inner whorls; become stronger and less approximated on body-chamber, retaining the low furcation.

Body-chamber just over half a whorl in length, peristome bears characteristic apertural horn (though not well displayed on the specimen) which is ribbed with maximum ventral projection of 3.5 mm. Marked uncoiling of the umbilical seam over length of body-chamber.

Remarks. This specimen differs from *P*. (*P*.) *devillei* in being considerably more evolute, although this is exaggerated by the crushing which has elongated the umbilicus. It is also more coarsely ribbed on the outer whorl than the type specimen. There are, however, sufficient similarities to *P*. (*P*.) *devillei* to determine that this specimen is closely related. It differs very considerably in rib style, degree of evolution and horn development from *P*. (*P*.) *circunligatus* described immediately below.

Pectinatites (Pectinatites) circumligatus sp. nov.

Plate 45, fig. 2

Diagnosis. Microconch *Pectinatites* approximately 80 mm in diameter with the following approximate rib densities; at 20 mm diameter, 40 ribs; at 25 mm, 36;

30 mm, 33. Ribs slender, often rursiradiate at umbilical shoulder, otherwise rectiradiate to prorsiradiate. Outer whorl with occasional simple and polygyrate ribs and narrow constrictions. Peristome with ventral horn.

Holotype, NMW 77.12G.12, the only specimen.

Horizon. 3.65 m below Bed 2. Upper Kimmeridgian, pallasioides Zone, upper part.

Description. Specimen 82 mm in diameter, umbilical diameter 33 mm. There are thirty-eight primary and about sixty-two secondary ribs on the last whorl. Inner whorls not well preserved and rib densities (see Diagnosis) therefore approximate. Ribs fine, slender throughout; rursiradiate to umbilical shoulder where they become rectiradiate to prorsiradiate. Umbilical seam uncoils over last half whorl which appears to correspond to length of body-chamber. On body-chamber ribs mainly bifurcate, though there are seven simple and one polygyrate rib. Intercalatory secondary ribs rare, only one identified with certainty.

On outer whorl narrow constrictions occur (apparently absent on inner whorls); four on this specimen, each bounded to front by a simple rib, but preceding rib may be simple, bifurcate, or polygyrate. Peristome bears a horn, partly broken; preserved portion has ventral projection of about 5 mm.

Remarks. This single specimen is the stratigraphically highest ammonite of the genus *Pectinatites* hitherto recorded in Britain. It is over 12 m higher in the Dorset succession than the specimen described as *P. (P.)* cf. *devillei* above (p. 487). It is accompanied in Dorset by various species of *Pavlovia*, from which it is immediately distinguished by the much denser and more delicate ribbing, particularly on the body-chamber, and by the horned peristome. Constrictions appear generally to be an infrequent character of *Pectinatites*, but are quite common in the subgenus *Virgatosphinctoides* (see Cope 1967) which has not, however, been certainly identified from horizons above the *hudlestoni* Zone.

There is some resemblance to *P*. (*P*.) *boidini* (de Loriol) which came from the Tour Croi Nodule Bed of the Boulonnais and could thus be of similar age. This latter species (figured de Loriol 1875, pl. 7, fig. 1) shows some resemblance in rib style to *P*. (*P*.) *circunligatus*, but is more finely ribbed and the apertural region is unknown. The holotype of *P*. *boidini* is so incomplete that it would need the collection of good topotype material to satisfactorily interpret the name.

Subfamily PAVLOVIINAE Spath, 1931 Genus PAVLOVIA Ilovaisky, 1917

Type species (subsequent designation, Spath 1931). Pavlovia iatrensis var. primaria Ilovaisky, 1917.

Discussion. The name *Pavlovia* is the senior available name for Upper Kimmeridgian (and Portlandian) ammonites bearing regular bifurcating ribs to the aperture, and with occasional constrictions generally preceded by some type of compound rib and succeeded by a simple unbranched primary rib. These were described under a variety of generic names by Buckman, Neaverson, and Spath. The late recognition of *Pavlovia* in Britain stems from the fact that Ilovaisky's (1917) monograph was unknown here for several years. The type species was not designated by Ilovaisky, who never completed work on the monograph; several species and many 'varieties' were named and figured in the published part, but only some of them described.

Spath (1931, p. 471) considered that *Pavlovia* 'must be interpreted by *P. iatrensis* var. *primaria* Ilovaisky' and this has subsequently been regarded as designation of the latter form as type species of the genus (Arkell, 1957, p. L332). It is now becoming

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apparent that in addition to being one of the most characteristic of the late Kimmeridgian ammonites from the Boreal faunal province (and probably the only one all the subprovinces have in common), the genus persisted little-changed well into Portlandian times, and such genera as *Crendonites* and *Glaucolithites* are clearly very closely related to *Pavlovia*. It is intended to figure these later forms in a description of the Portland Sand ammonite faunas in the future.

Dimorphism of Pavlovia

In common with all other perisphinctid ammonites, *Pavlovia* exhibits dimorphism, which is readily apparent in large collections, where mature ammonites fall into two size groups. In many other perisphinctid genera the aperture is often modified at maturity with a process of some sort. Thus the microconchs of most Oxfordian and Lower Kimmeridgian perisphinctids have a pair of lappets at the peristome, while the ribbing of the body-chamber of the macroconch is often significantly coarser and may be modified in various ways. In the Upper Kimmeridgian genus *Pectinatites* the microconch bears a ventral horn (see Cope 1967 and this paper for illustrations).

In *Pavlovia* no such apertural modification of the microconchs is usually apparent and the macroconchs do not exhibit any marked variocostation. The fact that most of the ammonites described here are crushed, renders what little apertural modification there may be almost impossible to detect. In some of the uncrushed material from the Rotunda Nodule Bed some apertural modification is visible and some specimens may show lateral flaring of the peristome margin, whilst others may have a ventral peristomal inflation (see Pl. 51).

The absence of any marked peristomal modification renders distinction of the dimorphs difficult in some cases. It is readily apparent that some forms are microconchs because of size considerations. Others must equally be macroconchs. The difficulty lies particularly with one or two groups of intermediate-sized forms from horizons yielding, in addition to these, obvious microconch forms and exceptionally large macroconchs. Are these intermediate-sized forms, clearly mature ammonites, macroconchs of the small microconchs or are they microconchs of the very large forms? In the case of *Pectinatites* a definite relationship was found between rib-densities of microconchs and macroconchs (Cope 1967). No such clear relationship appears to exist in *Pavlovia*. This raises taxonomic problems. In my earlier treatment of *Pectinatites* I was able to group together microconch and macroconch forms for most of the same species could be 'paired off' and a single specific name accorded to the two forms. Clearly this arrangement is the one to aim for—where morphospecies are believed to approximate to biospecies. With *Pavlovia* (at least with the faunas described here), this does not appear possible. In some cases probable associations can be suggested, but not with the same confidence as for species of *Pectinatites*.

There remain two possible methods of dealing with this problem taxonomically. First, there is the use of subgeneric names as advocated by Callomon (1963). His use of subgenera to distinguish microconch and macroconch certainly has its attractions; it is convenient and solves any problems in matching dimorphs, but raises other problems. What happens when it is impossible to determine whether a particular specimen is a microconch or a macroconch? Presumably one must then revert to a simple binomen. The use of subgeneric names in this context also raises other problems and precludes the use of a subgenus as a useful infra-generic but supra-specific rank, which sexual distinction is not. The second taxonomic solution is to accord dimorphs different specific names (this is necessary under Callomon's procedure too), which are, however, retained in the same genus and subgenus. If 'pairs' of ammonites can subsequently be made the problem is resolved by placing the junior name into synonymy. The advantages of this second method appear to far outweigh its disadvantages and accordingly I have described the dimorphs of species of *Pavlovia* under separate specific names.

The origins of Pavlovia

It has been customary for many years to look to earlier Kimmeridgian evolute round-whorled ammonites as the ancestors of *Pavlovia*. Spath believed in a 'conservative root-stock' of such forms giving rise periodically to more rapidly evolving forms. These ancestral types were believed to include, in Kimmeridgian times, the genus *Subdichotomoceras* (type species *S. lamplughi* Spath, 1925). Thus, Arkell (1957, p. L332) stated that the pavloviids were probably developed from *Subdichotomoceras*.

In seeking the origins of *Pectinatites* I noted that the presence of polygyrate furcation of the ribs was believed to yield a clue, in that this feature was unknown until Upper Oxfordian times, and that ammonites with polygyrate ribbing thus probably had a common ancestry (Cope 1967, p. 23). *Subdichotomoceras* is devoid of such furcation style, whilst it is immediately obvious that it occurs in *Pavlovia*.

I consider that the *paravirgatus* Subzone of the *pectinatus* Zone has now yielded the answer, as in Dorset the ammonites of this subzone appear to show a transition from *Pectinatites* to *Pavlovia*, through forms previously included in the genus *Paravirgatites* (see pp. 476–485). The horned microconch of *Pectinatites* gradually lost the horn and the ribbing of the body-chamber of the macroconch simultaneously became coarser and more *Pavlovia*-like. Thus one could claim that the polygyrate ribbing seen in most species of *Pavlovia* betrays the pectinatitid ancestry of the group. One could also suggest that the ventral inflation of the ventral part of the peristome in some *Pavlovia* microconchs and the finely ribbed inner whorls of some species are other evidences of the origins of the genus. This implies palingenesis which is an unfashionable idea in ammonite palaeontology; the opposite idea of proterogenesis seems to hold more sway (despite the recent rejection of some commonly quoted examples). It may be noted, however, that the finely ribbed inner whorls of *Pavlovia* are not seen to ornament the body-chamber of any later forms.

There follows below a discussion of generic names which have been applied in the past to ammonite species considered here to belong to the genus *Pavlovia*.

LYDISTRATITES Buckman, 1922; type species L. lyditicus Buckman, 1922

This name is one of the most misinterpreted of Buckman's genera, largely because he figured three completely unrelated forms as examples of the type species; he believed that the Upper Lydite Bed was a constant horizon and accorded the '*lyditicus*' fauna hemeral status. In view of this confusion I discuss here all the forms that Buckman included in the genus.

The holotype of the type species (Buckman 1922, pl. 353A) came from the Upper Lydite Bed at Long Crendon, Buckinghamshire, and is clearly a pavloviid. It is large (255 mm diameter) and incomplete. Buckman suggested that the present termination of the shell might have been the last septum, in which case only the body-chamber (probably one-half to five-eighths of a whorl) is missing. The rib style and furcation combined with the size suggest strongly that the specimen is a Portlandian rather than a Kimmeridgian pavloviid. Similar forms occur in Dorset in the upper part of the Portland Sand and confirm that the Upper Lydite Bed at Long Crendon embraces a major non-sequence. I do not accept the suggestion that the specimen could be an *Epivirgatites* (Casey 1967, p. 132). The horizon at which similar forms occur in Dorset suggests that the specimen requires correlation with horizons well above the *albani* Zone. *Epivirgatites* is, as far as is known at present, confined in Britain to the *albani* Zone.

Buckman's paratype (1922, pl. 353B) bears no relation to the holotype; it came from the Upper Lydite Bed at Swindon. The rib style of this form confirms that this specimen belongs properly in *Progalbanites*, as Casey (1967, p. 132) suggested.

The other specimen figured as *L. lyditicus* by Buckman (1926, pls. 353C, 353D) is a *Pavlovia* from the Rotunda Nodule Bed at Chapman's Pool, here included in *P. rotunda* (see p. 512).

Buckman also included other unrelated ammonites in *Lydistratites*. *L. biformis* (1925, pls. 605A, 605B) appears, to judge from the presence of virgatotome ribs with up to five secondaries on the inner whorls, to belong to *Progalbanites*, though Casey (1967, p. 132) thought it to be an *Epivirgatites*. However, at least on British material, ribs more complex than polygyrate are not usual on the inner whorls of *Epivirgatites* while the outer whorls show four-branched ribs associated only with constrictions (see Pl. 55, figs. 2, 3). *L. cunctator* (1925, pls. 606A, 606B) is based on the inner whorls of indeterminate pavloviids or possibly of *Progalbanites*. *L. gibbosus* (1926, pls. 639A–C; 1927, pl. 639D) and *L. trigonalis* (1926, pls. 674A, 674B) are macroconch forms of *Pavlovia* from the Rotunda Nodule Bed. The triangular whorl section of the latter species may be due entirely to post-mortem distortion of the shell and the specimen is otherwise like *L. gibbosus*. Both are here included in *P. rotunda* (see p. 512).

The name *Lydistratites* must, however, be interpreted by the holotype of the type species and it seems best therefore to treat *Lydistratites* as a junior synonym of *Pavlovia*, pending further work on the pavloviids of the Portland Sand.

PALLASICERAS Spath, 1924; type species Ammonites rotundus Sowerby, 1821

Spath proposed *Pallasiceras* for ammonites characterized by finely ribbed inner whorls, but with an outer whorl with coarse bifurcate ribs and occasional constrictions. Spath also stated that the genus had a

depressed whorl section. At the time of foundation of the genus, Spath was unaware of the existence of Ilovaisky's (1917) monograph on *Pavlovia*. He later came to regard *Pallasiceras* as only subgenerically distinct from *Pavlovia*. The characteristic of *Pallasiceras* so immediately noticeable in most of the species subsequently ascribed to it (e.g. *P. pringlei* Neaverson) is the dense ribbing on the inner whorls, though this character is not shown to the same extent in the type species. At the Rotunda Nodule Bed horizon, *Pallasiceras* does appear to be a distinct form, readily separable from most of the pavlovids of the *pallasioides* Zone below. However, intervening beds in Dorset, apparently absent from other areas of Britain, and the description of new *Pavlovia* faunas from both the *pallasioides* and *rotunda* Zones, show that there is no sharp line of separation between *Pallasiceras* and *Pavlovia* and that recognition of *Pallasiceras* as a subgenus of *Pavlovia* is of doubtful value. The depressed whorl section mentioned by Spath as a character of *Pallasiceras* is not believed to be of any diagnostic value in pavlovid classification above specific level. *Pallasiceras* is therefore treated here as a junior synonym of *Pavlovia*.

HOLCOSPHINCTES Neaverson, 1924; type species H. pallasioides Neaverson, 1924

Neaverson (1925) figured two species of this genus which he described as evolute forms with a shallow umbilicus. The inner whorls were said to be finely ribbed with a marked forward inclination of the ribs. Constrictions were 'not numerous' and shallow (Neaverson 1925, p. 33). The similarity between Neaverson's species and some of the species of *Pavlovia* figured by Ilovaisky (1917) is very great, and there is no doubt that *H. pallasioides* is a *Pavlovia* in the strictest sense. The characters of *Holcosphinctes* were admitted to show 'a striking degree of homeomorphy' (Neaverson 1925, p. 34) with *Aposphinctoceras* and *Pallasiceras* and the fact that all three 'genera' occurred in the same horizon and locality confirms the view that the species may be allotted to a single genus—in this case *Pavlovia*. *Holcosphinctes* is thus treated here as a junior synonym of *Pavlovia*.

APOSPHINCTOCERAS Neaverson, 1924; type species A. decipiens Neaverson, 1924 (=Olcostephanus pallasianus (d'Orbigny) var. Healey, 1904).

The type, and only known specimen of the type species, came from the Upper Kimmeridge Clay of Chippinghurst near Chiselhampton, a locality in which there are now no exposures of the Kimmeridge Clay. Neaverson's statement that it came from the *pallasioides* Zone (1924, p. 149) was accepted by Arkell (1947b, p. 108) without comment, though there is no evidence that the specimen was not from the *rotunda* Zone.

Neaverson described three other species of *Aposphinctoceras* in his monograph, all from the Hartwell Clay (i.e. *pallasioides* Zone). His criteria for distinction of the genus were the straight sweep of the secondary ribs over the venter, and the coarsely ribbed inner whorls. The first of these criteria does not appear to me to be a valid cause for distinction, as this character is seen in large collections to vary in degree from individual to individual within any given species, and often varies too in an individual during its development. The second criterion is readily dismissed on perusal of Neaverson's own figures. Thus *A. ailesburiense* (Neaverson 1925, p. 27, pl. 2, fig. 3), which incidentally is the only specimen of *Aposphinctoceras* figured by Neaverson which shows the inner whorls at all well, is scarcely coarser ribbed than *Pallasiceras rotundum* (Neaverson 1925, p. 18, pl. 1, fig. 6).

In view of these facts and Neaverson's admission of the homeomorphy of *Aposphinctoceras* with both *Pallasiceras* and *Holcosphinctoceras*, there seems no justification for the recognition of *Aposphinctoceras* as a separate taxonomic unit either at generic or at subgeneric level and it appears best to treat this form too as a junior synonym of *Pavlovia*.

EPISPHINCTOCERAS Neaverson, 1925; type species E. inflatum Neaverson, 1925

The type specimen of this monotypic genus came from the lower part of the Hartwell Clay, supposed by Neaverson to belong to the *rotunda* Zone, but now known to be from the lower part of the *pallasioides* Zone (the stratigraphical relationship between the *pallasioides* and *rotunda* zones was incorrectly determined by Neaverson). Thus Neaverson's statement (1925, p. 24) that *Episphinctoceras* occurred only in the *rotundum* Zone needs reinterpreting.

The holotype was an unfortunate choice, for it shows one whorl of an obviously incomplete shell. Neaverson suggested that almost one whorl was missing, giving an adult diameter of around 170 mm. Unfortunately, too, the inner whorls are unknown on the specimen, though Neaverson mentioned that they show a coarse-ribbed character beyond a diameter of 3 mm; this feature must have been shown by another specimen and it is a great pity that no evidence was figured on this point. The holotype shows a typical pavloviid rib style—fairly regular bifurcating ribs with a few simple ribs and the usual occasional constrictions. These are preceded by a bidichotomous rib (a type of polypoke furcation with the first bifurcation very low on the whorl side) and succeeded by a simple rib.

One may, of course, only guess at the characters of the missing whorls of the holotype and it seems that the name may never be fully interpreted. Spath (1936, p. 27) was of the opinion that the inflated whorl section was due, in no small measure, to oxidation of the pyrite on the outer whorl and was not an original feature. Certainly the size of the specimen suggests that it is a macroconch and it could be conspecific with macroconch forms described here from the *pallasioides* Zone of Dorset. However, the specimen cannot be matched with certainty with any other known form and should never have been used to serve as type material for a new genus. *Pavlovia* already includes forms very little different from *Episphinctoceras* and this genus is therefore treated as a junior synonym of *Pavlovia*.

In the systematic treatment of species of *Pavlovia* which follows below, the descriptions are arranged as far as possible in ascending stratigraphical order, although where ranges of species overlap this may not always appear clear.

Pavlovia sp. A

Text-fig. 6

Material. One specimen (NMW 77.12G.48).

Horizon. 3.5 m above base of Bed 3. Upper Kimmeridgian, pallasioides Zone, lower part.

Description. The specimen is incomplete; its largest preserved diameter is approximately 325 mm; there, umbilical diameter is 148 mm. When complete the specimen was at least 360 mm in diameter, and at a point corresponding to that diameter, the umbilicus measures 170 mm across. At 30 mm diameter there are an estimated 26 ribs; at 40 mm, 26; 50 mm, 28; 60 mm, 30; 70 mm, 31; 80 mm, 32; 90 mm, 32; 100 mm, 32; 110 mm, 33; 120 mm, 33; 130 mm, 33; 140 mm, 34; 150 mm, 34; 160 mm, 34; 170 mm, 33. The last preserved whorl has 33 primary and an estimated 60 secondary ribs.

Ribs on inner whorls rectiradiate to prorsiradiate; many concave (towards the aperture). Occasional ribs show very low furcation, but otherwise bifurcation hard by umbilical seam of succeeding whorl. Ribs rounded in cross-section, not acutely sided as in *Pectinatites* in beds below.

Over last umbilical whorl ribs become more widely spaced and blunt, until on outer whorl they are quite gentle folds in the shell wall; though retaining a discrete rib shape, their cross-section has much shallowerangled sides. Secondary ribs also lose prominence; on body-chamber fade significantly. Towards the mouth there is simplification of ribbing and frequent unbranched primary ribs and intercalatory secondaries.

The specimen has been distorted by joints which have caused dislocation of part of the outer and the last umbilical whorl. There is no indication of length of body-chamber.

Remarks. The coiling of this specimen is very evolute, and even though the central part of the umbilicus is not preserved, almost seven whorls of shell are visible. It is this feature which provides very clear distinction from other species of the genus, at whatever their horizon. Although the beds of the *pectinatus* Zone only a little below yield several large species of ammonites, they are all pectinatitids and with a markedly different rib shape and style are not likely to be confused with this species. It is also the stratigraphically oldest *Pavlovia*, occurring some 7 m lower than the next (identifiable) pavloviid (see text-fig. 11).

Pavlovia composita sp. nov.

Plate 48, fig. 3

Diagnosis. Macroconch *Pavlovia* 127–151 mm diameter, with following rib densities: at 15 mm 26–30 ribs; at 20 mm, 26–30; 25 mm, 26–29; 30 mm, 26–29; 35 mm, 25–30;

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TEXT-FIG. 6. *Pavlovia* sp. A. NMW 77.12G.48, Bed 3b, 3.5 m above top of Bed 4. $\times 0.48$.

40 mm, 26–32; 45 mm, 26–32; 50 mm, 26–32; 55 mm, 25–33; 60 mm, 28–31; 65 mm, 28–31. Ribs on inner whorls straight to gently curved, rursiradiate to prorsiradiate. Outer whorl with thicker rectiradiate to prorsiradiate ribs, mainly bifurcate but occasional simple and intercalatory ribs; polygyrate ribs rare. Peristome simple. Occasional constrictions, usually one near peristome.

Holotype, NMW 77.12G.32; Paratypes, NMW 77.12G.22-31, 33, 34, 36, 37, 40, 41.

Horizon. Holotype from Bed 3d at 8.5 m below Bed 2.

Stratigraphical range. Upper Kimmeridgian, *pallasioides* Zone, ranging from 15.25 to 4.50 m below Bed 2 (Beds 3b-3h).

Description. Shell moderately to very evolute, from 127 to 151 mm in diameter. Umbilical diameter 50–69 mm. The holotype has a diameter of 133 mm and an umbilical diameter of 57 mm; it has thirty-six primary and sixty-nine secondary ribs on the outer whorl. On the holotype it is not until a diameter of 30 mm that it is possible to accurately determine rib densities. At that diameter there are twenty-nine ribs; for densities beyond that see Diagnosis (above). Secondary ribs not visible within the umbilicus on the holotype. Some of the paratypes are, however, more evolute. Over the last quarter of a whorl there is quite a marked uncoiling of the umbilical seam on the holotype, but even then the furcation point of the ribs is not fully exposed.

Some paratypes show very close associations of ribs on inner whorls which suggest constrictions, although crushing renders precise determination impossible.

On outer whorl ribs become stronger, sharply delineated; predominantly bifurcate, with occasional simple ribs (three on holotype) and intercalatory secondary ribs. Polygyrate ribs and polyploke ribs are rare and almost entirely confined to the rib immediately preceding a constriction. Most specimens have at least one, and up to three, constrictions on the last whorl. Constrictions are of two types: 1, wide constrictions, usually following a polygyrate or a polyploke rib and succeeded by a simple rib; 2, narrow constrictions, usually preceded by a bifurcate rib and followed very closely by a simple rib. This latter rib may be quite prominently flared laterally and have a noticeable ventral protuberance. Most specimens appear to have a constriction of type 2 just a little back from the peristome. The peristome itself is smooth and the immediately preceding ribs less pronounced than those on the rest of the shell. Differences in the degree of crushing suggest that the body-chamber is between three-fifths and three-quarters of a whorl in length.

Remarks. This species appears quite distinct from any species of *Pavlovia* described hitherto. The closest comparison is with the Russian species *P. menneri* Michailov (1966, pl. 14, fig. 1) which is, however, more coarsely and a little more regularly ribbed. It differs from *P. superba* sp. nov. (p. 498) in being considerably smaller in diameter (mean diameter of *P. composita*, 135 mm; mean diameter of *P. superba*, 221 mm). The differences from *P. rotunda*, which is apparently confined to the overlying *rotunda* Zone, are in rib density and mature size. *P. rotunda* is considerably more densely ribbed at small diameters than *P. composita*, though later rib densities on the inner whorls are similar. *P. rotunda* has a somewhat smaller mature diameter. However, the earliest forms of *P. rotunda* are not as finely ribbed as later forms (see p. 512) and *P. composita* may have been on the direct line of descent to *P. rotunda*.

Pavlovia composita waddingtoni subsp. nov.

Plate 49, fig. 1

Diagnosis. Macroconch *Pavlovia* around 185 mm diameter with the following rib densities: at 30 mm diameter there are 33 ribs; at 35 mm, 33; 40 mm, 32; 45 mm, 31–32; 50 mm, 31–32; 60 mm, 32; 70 mm, 34–35; 80 mm, 37. Ribs on innermost

EXPLANATION OF PLATE 48

Fig. 3. P. composita sp. nov. Holotype, NMW 77.12G.32, ×1. Bed 3d, 8.5 m below Bed 2.

Fig. 1. Pavlovia sp. nov. aff. raricostata Ilovaisky. NMW 77.12G.84, ×1. Bed 2.

Fig. 2. *P. concinna* (Neaverson). NMW 77.12G.55, $\times 1$. 0.9 m above Bed 2.



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whorls dense, fine, prorsiradiate. Middle whorls with thicker ribs, rectiradiate to prorsiradiate, bifurcation frequently low and visible. Outer whorl also with low furcation, ribs thicker, blunter, predominantly bifurcate; occasional constrictions.

Holotype, NMW 77.12G.35; Paratypes, NMW 77.12G.42-44.

Horizon. Holotype from Bed 3g at 5.5 m below Bed 2.

Stratigraphical range. Upper Kimmeridgian, pallasioides Zone, ranging from 6·1 m to 4·5 m below Bed 2 (Beds 3g and 3h).

Description. Shell evolute, diameter about 185 mm. No complete specimen has been found, but the holotype appears to be virtually complete at that diameter. Umbilical diameter of holotype 85 mm, and an estimated thirty-eight primary and seventy-six secondary ribs on outer whorl. For rib densities see Diagnosis (above). Ribs on innermost whorls fine and slender, closely crowded, prorsiradiate. At a diameter of 15 mm at least forty ribs; then a sharp drop in rib density to thirty-three at 30 mm. Bifurcation point low enough to render it visible. Ribs become less slender, still mainly prorsiradiate, on middle whorls. Outer whorl ribs considerably stronger on body-chamber, which bears stout, blunt, primary ribs, virtually all bifurcate. Occasional constrictions, at least one on outer whorl of holotype. Polygyrate and simple ribs seem confined to vicinity of constrictions. Degree of crushing suggests that body-chamber length was between three-fifths and three-quarters of a whorl.

The peristome is not preserved on any specimen.

Remarks. This subspecies appears to be considerably larger in mature size than *P. composita s.s.*, but shares with it similar (though not identical) rib density, and a closely similar rib style. The differences in size might be considered to be such as to provide distinction at specific level. However, in view of the fact that only one really adequate specimen of this form has been obtained, it is thought better to include these forms within *P. composita*, but recognizing a subspecific distinction.

The rib density of the inner whorls of this subspecies shows a feature that is much more typical of species of *Pavlovia* from the overlying *rotunda* Zone, in that the rib density of the inner whorls decreases sharply initially and then remains at a fairly constant level, sometimes rising again later. This character is one found particularly in forms which Spath included in his genus (later subgenus) *Pallasiceras*. He did not, however, mention this feature as characteristic of *Pallasiceras*, and the usefulness of the name, even at subgeneric level, is doubtful (see p. 490).

This subspecies does therefore, in respect of rib density, show some similarity with *P. rotunda*. It differs from the latter species, however, in mature size, rib style, and has not the same rib density.

Other species from the *pallasioides* Zone may be readily distinguished from *P. composita waddingtoni* by characters of mature size, rib style (particularly on the innermost whorls), and rib density. It is, for instance, considerably finer ribbed on the outer whorl than *P. superba* at a comparable diameter.

EXPLANATION OF PLATE 49

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Fig. 1. Pavlovia composita waddingtoni subsp. nov. Holotype, NMW 77.12G.35, ×0.85. Bed 3g, 5.5 m below Bed 2.

Figs. 2, 3. *P. concinna* (Neaverson). NMW 77.12G.51, 77.12G.64, ×1. Bed 2.



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Pavlovia superba sp. nov.

Text-fig. 7

Diagnosis. Large macroconch *Pavlovia* with following rib densities: at 15 mm, 27–29 ribs; 20 mm, 27–30; 25 mm, 27–30; 30 mm, 27–31; 35 mm, 27–32; 40 mm, 27–31; 45 mm, 27–30; 50 mm, 28–29; 55 mm, 28–29; 60 mm, 28–30; 70 mm, 28–31; 80 mm, 28–31; 90 mm, 28–32; 100 mm, 29–32. Ribs on innermost whorls slender, prorsiradiate from umbilical shoulder. Later whorls with stouter more rectiradiate ribs; on outer whorl strong well-spaced primaries, mainly bifurcate, occasional simple, intercalatory and polygyrate ribs. Few constrictions. Peristome simple.

Holotype, NMW 77.12G.77; Paratypes, NMW 77.12G.78-83.

Horizon. Holotype from Bed 3d at 10.65 m below Bed 2.

Stratigraphical range. Upper Kimmeridgian, *pallasioides* Zone, ranging from 11.0 m to 6.5 m below Bed 2 (Beds 3d–3g).

Description. Shell evolute, diameter 210-242 mm. Umbilical diameter 94-115 mm. Holotype has a diameter of 242 mm and umbilical diameter of 115 mm. There are thirty-five primary and seventy-nine secondary ribs on the last whorl of the holotype. For rib densities see Diagnosis (above). The variation in rib density is shown in text-fig. 9.

With increasing diameter the ribs become progressively stouter and lose the pectinatitid slenderness of the innermost whorls. Point of bifurcation high, not visible within umbilicus except over the last one-fifth of a whorl where uncoiling of the umbilical seam becomes marked. Constrictions not discernible on inner whorls.

Outer whorl of holotype has one constriction, situated about one-eighth of way round last whorl, preceded by a polygyrate rib and followed by a simple unbranched primary rib. Primary ribs on outer whorl stout, becoming more widely spaced. There is, however, no real variocostation in this species, rib spacing increases regularly with diameter, so that figures for rib density remain remarkably constant with increasing diameter. Outer whorl ribs predominantly bifurcate, towards aperture more polygyrate furcations occur, whereas on the earlier part of the last whorl intercalatory ribs are more common between the bifurcate ribs. Some paratypes are more coarsely ribbed on outer whorl; they have comparable density of primary ribs to that of the holotype, but fewer secondary ribs.

Differences in the degree of crushing suggest that the body-chamber was just over three-quarters of a whorl in length. In three specimens the presumed position of the last septum coincides with a constriction. Peristome not preserved completely on any one specimen and is probably best preserved on the holotype. It is smooth and with a suggestion of a slight outward flare.

Remarks. Other large species of *Pavlovia* may be readily distinguished from this form. *P. kochi* Spath (1936, p. 50, pl. 15, fig. 1) is considerably larger than this form, and is noticeably more densely ribbed at comparable diameters. *P. variabilis* Spath (1936, p. 48, pl. 10, fig. 1) is smaller (even allowing for the increase in diameter of the Dorset

EXPLANATION OF PLATE 50

Fig. 1. Pavlovia pallasioides (Neaverson). NMW 77.12G.39, ×1. Bed 3e, 7.6 m below Bed 2.

Fig. 3. *P. rotunda gibbosa* (Buckman). BMC C.74670, $\times 1$. Rotunda Nodule Bed. The specimen appears to consist virtually entirely of phragmocone. Note that the ornament is malformed on the last quarter of the final (preserved) whorl.

Fig. 2. P. concinna (Neaverson). NMW 77.12G.54, ×1. Bed 1, 1 m above Bed 2.



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TEXT-FIG. 7. Pavlovia superba sp. nov. Holotype, NMW 77.12G.77, Bed 3d at 10.65 m below Bed 2. $\times 0.65$.

forms due to crushing) and is somewhat more crudely ribbed; it is apparently stratigraphically younger, and according to Spath is of *rotunda* Zone age. When Spath (1936) wrote this, however, the *pallasioides* Zone fauna was believed to be younger than the *rotunda* Zone fauna; it is thus possible that *P. variabilis* is of similar age to *P. superba*. The relationship of this species to the problematical *Episphinctoceras inflatum* Neaverson is more difficult to determine. They are presumably of approxi-

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mately the same age, but as mentioned earlier (p. 491), Neaverson's specimen is so poor that interpretation is impossible. Only one large specimen of *Pavlovia* has hitherto been figured from Russia. Michailov (1966, p. 59, pl. 18, fig. 1) figured a specimen as *P*. aff. *kochi* Spath, but this specimen appears to me to resemble much more closely certain species of the genus *Dorsoplanites* such as *D. maximus* Spath or *D. jamesoni* Spath, and indeed the suture line figured by Michailov (1966, text-fig. 28) is much closer to that of some of the *Dorsoplanites* that he figures, than to any of his *Pavlovia*.

Pavlovia pallasioides (Neaverson, 1924)

Plate 50, fig. 1; Plate 52, fig. 4; Plate 53, figs. 1, 4

1895 Ammonites biplex auctt. (non Sow.); Woodward, p. 156, fig. 72.

- 1924 Holcosphinctes pallasioides Neaverson, p. 149.
- 1925 Holcosphinctes pallasioides Neaverson; Buckman, pl. 569.
- 1925 Aposphinctoceras ailesburiense Neaverson, p. 27, pl. 2, fig. 3.
- 1925 Aposphinctoceras hartwellense Neaverson, p. 28, pl. 2, fig. 4.
- 1925 Aposphinctoceras variabile Neaverson, p. 29, pl. 2, fig. 5.
- 1925 Holcosphinctes pallasioides Neaverson; Neaverson: 35, pl. 3, fig. 5.
- 1933 Pavlovia pallasioides (Neaverson) Arkell, p. 440.
- 1956 Pavlovia pallasioides (Neaverson); Arkell, pl. 41, fig. 4.

Material. Twenty-one specimens.

Stratigraphical range. Upper Kimmeridgian, *pallasioides* Zone, ranging from 13.4 m to 1.8 m below Bed 2 (Beds 3d–3h).

Description. There is a very good agreement between specimens from Chapman's Pool and the holotype which came from the Hartwell Clay of Hartwell. Diameter of shell ranges from 74 to 105 mm (crushed) and umbilical diameter from 29 to 41 mm. Rib densities of inner whorls as follows: at 15 mm diameter, 26-30 ribs; at 20 mm, 26-31; 25 mm, 25-31; 30 mm, 24-29; 35 mm, 28-29; 40 mm, 28. The outer whorl has 29-33 primary ribs and 51-68 secondary ribs. The largest specimen figured here (NMW 77.12G.69) has an intact peristome with a distinct anterior projection towards the ventral area. This specimen shows several polygyrate ribs on the last whorl; the lower of the two furcations on these ribs occurs at same point on whorl side as normal point of bifurcation. The one exception to this is about one-fifth of a whorl back from the peristome where a polygyrate rib has its initial furcation very low on the whorl side; this rib is succeeded by a simple unbranched primary rib, and the association of these two rib types in this fashion strongly suggests that there was a constriction at this point, though evidently it was a very shallow one. Neaverson's description (1925, p. 35) states that 'constrictions are few in number and do not interrupt the normal course of ribbing, being neither conspicuously wide nor deep'. With crushed ammonites constrictions are not easily discernible and in the case of their feeble development, detection would be that much more difficult. Another figured specimen (NMW 77.12G.70) also shows similar rib development a little distance back from the mouth (not the peristome-which is not preserved on this specimen) of the shell. This specimen too shows other polygyrate ribs on the last whorl. Body-chamber length of the specimens appears to be about five-eighths of a whorl.

Remarks. Neaverson's description (1925, p. 35) contains erroneous dimensions of the holotype. The diameter is 81 mm and not 71 mm (nor 83 mm as the 'natural size' plate suggests). The umbilical diameter of 37.5 mm is 46.5% of this figure suggesting a typographical error in the figure given for the diameter. However, the last part of the body-chamber of the holotype is partially crushed so that figures and whorl height and thickness cannot be determined. The latest point at which the shell is uncrushed is at a diameter of 71 mm so that this figure may have been used by Neaverson as

a basis for his dimensions. However, measurements I have made on the holotype suggest errors here too. There are thirty-one primary ribs on the last whorl of the holotype, and an estimated fifty-nine secondary ribs (part of the last whorl is not well preserved). Rib density measurements on the inner whorls, a partial impression of which is preserved, suggest that at 20 mm diameter there are 30 ribs; at 25 mm, 30; and at 35 mm, 29. These rib density figures agree well with the figures given above for the Dorset specimens.

The various specimens which Neaverson described under his generic name *Aposphinctoceras* also seem to belong quite clearly to this species. As mentioned earlier *Aposphinctoceras* is clearly a *Pavlovia* and the various species of it described by Neaverson seem to fall within the range of variation in *P. pallasioides* (see text-fig. 10).

In the summer of 1972 I had the opportunity to collect from the Hartwell Clay in a large temporary excavation in Aylesbury, and have also examined the collections made there by Mr. M. Oates who kindly informed me of the exposure. Some 4 m below the Upper Lydite Bed there was a horizon yielding the typical beautiful irridescent ammonites of the Hartwell Clay. Amongst these were typical P. pallasioides (see Oates 1974 for illustrations). Most of the specimens of this species which I collected there show constrictions, always preceded by a polygyrate rib and followed by a simple rib in typical Pavlovia fashion. Neaverson's statement that the constrictions do not interrupt the normal course of ribbing is open to criticism. Half a whorl back from the aperture of the holotype may be seen a polygyrate rib-constrictionsimple rib association. The reverse side of the specimen, however, shows the progression bifurcate rib-constriction-simple rib. The posterior secondary rib of the polygyrate rib becomes the anterior secondary of the preceding bifurcate rib on the other side of the ammonite, and for some way back the secondary ribs zigzag over the venter-a feature which occurs quite commonly in *Pavlovia* and is a character of no specific significance.

There is a striking resemblance between some of the forms figured by Ilovaisky (1917) and *P. pallasioides*. Thus *P. paratropa* (Ilovaisky, pl. 3, fig. 2*a*) and *P. hypophantica* (Ilovaisky, pl. 3, fig. 1*a*) are close in many characters to *P. pallasioides*. The resemblance is so close that it could be suggested that *P. paratropa* and *P. pallasioides* are conspecific. However, it is felt that no useful purpose would be served by making *P. pallasioides* a junior synonym of *P. paratropa*. The similarity cannot be proved to be conspecificity and the name of *P. pallasioides* has become so engrained in the literature that a change is to be deprecated. There is also a resemblance to *P. pavlovi* (Michalski) (refigured Michailov 1966, pl. 14, fig. 2), but this latter species has more

EXPLANATION OF PLATE 51

All figs. $\times 1$.

Fig. 1. *Pavlovia concinna* (Neaverson). NMW 77.12G.118. Rotunda Nodule Bed. Note mature peristome with ventral protuberance, but note too that this is exaggerated by displacement along a vein.

Fig. 2. P. rotunda (Sowerby). Topotype, BM C.77957. Rotunda Nodule Bed.

Fig. 3a, b. P. rotunda gibbosa (Buckman). BM C.77954. Rotunda Nodule Bed. Specimen is entirely phragmocone.

Fig. 4a, b. P. concinna (Neaverson). NMW 77.12G.117. Rotunda Nodule Bed. Fig. 4b is oblique view showing lateral extension of peristome.



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densely ribbed inner whorls. There can be no doubt that *P. pallasioides* is a *Paylovia* in the strictest sense, close to the type species, and provides a firm basis for correlation with the Russian faunas.

The stratigraphical position of *P. pallasioides* in the Dorset succession has hitherto been in doubt. Neaverson placed the *pallasioides* Zone above his *rotundum* Zone really without any evidence for this super-position, and his conclusions were not questioned save by Buckman, who believed the *pallasioides* Zone to lie below the *pectinatus* Zone. Buckman's stand on his ideas on the stratigraphical position of the Hartwell Clay stems from his being deceived by a workman on the provenance of some *pallasioides* Zone ammonites (see Arkell 1933, pp. 465-466). Casey (1967) was the first to show that the *pallasioides* Zone lies below, and not above, the *rotunda* Zone. His conclusion was based on the occurrence of the *pectinatus* Zone below the Hartwell Clay and on the presence of *rotunda* Zone, but not *pallasioides* Zone, ammonites in the Upper Lydite Bed of the south Midlands.

Neaverson (1924, p. 149) had stated that 'the clays above the *rotundum* Zone have yielded ammonites similar to *H. pallasioides* (though in a poor state of preservation)'. Spath (1936, p. 161) also recorded ammonites from these highest beds of the Kimmeridge Clay but was of the opinion that although poorly preserved they did not resemble the Hartwell Clay fauna. A detailed and prolonged search of these beds has been made by the writer and although ammonites have been obtained at several horizons, none resembling *P. pallasioides* has been found. On the other hand, undoubted examples of this species occur much lower, below the *rotunda* Zone fauna, and range from 13.4 to 1.8 m below Bed 2.

Pavlovia aff. strajevskyi Ilovaisky, 1917

Plate 54, fig. 1

Material. One specimen (NMW 77.12G.85).

Horizon. Upper Kimmeridgian, pallasioides Zone, Bed 3d at 9 m below Bed 2.

Description. The single rather poorly preserved specimen is estimated to have been 68–70 mm in diameter when complete. Umbilical diameter 25 mm. At 15 mm diameter there are an estimated 25 ribs; at 20 mm, 21; 25 mm, 19. Coiling quite evolute, so that parts of at least five whorls are readily visible. Outer whorl ribs mainly bifurcate, but with occasional simple and two trifurcate ribs. Peristome partially preserved.

Remarks. The similarity to *P. strajevskyi* is great, with the specimen closely matching the neotype (Michailov 1966, pl. 19, fig. 5). There is little similarity to any British forms. It is far more coarsely ribbed than any *P. pallasioides*; rib density is similar to the specimen described below as *P.* sp. nov. aff. *raricostata* but the latter is

EXPLANATION OF PLATE 52

All figs. $\times 1$.

Figs. 1, 3, 5. *Pavlovia concinna* (Neaverson). BM C.77944, C.78148, C.77948. Rotunda Nodule Bed. Small variety of the species; figs. 1 and 5 show examples complete with peristomes.

Fig. 2. P. rotunda gibbosa (Buckman). NMW 77.12G.119. Rotunda Nodule Bed. Typical large phragmoconic specimen.

Fig. 4. P. pallasioides (Neaverson). NMW 77.12G.38. Bed 3d, 8.5 m below Bed 2.



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larger, and has a more densely ribbed outer whorl with altogether thicker and heavier ribs.

P. strajevskyi was first described from the Lyapin River area of the Pre-polar Urals by Ilovaisky (1917). Michailov (1962) founded the genus *Strajevskya*, with *P. strajevskyi* as type species, for pavloviids with trifurcate or quadrifurcate ribbing, a tendency to a depressed whorl section, and sutural distinctions. In my opinion these forms are merely the coarse-ribbed extremes of *Pavlovia*, and do not warrant separate generic status. Multi-furcate secondary ribs vary so widely in this genus that no taxonomic importance can be placed on them. I consider the sutural variation mentioned by Michailov to be a direct consequence of the depressed whorl section of these forms, and of no taxonomic significance. *P. strajevskyi* is connected to the typical *Pavlovia* of the type *P. paratropa* Ilovaisky by such forms as *P. raricostata* Ilovaisky emend. Michailov and *P. hypophantiformis* (Michailov).

The presence in Britain of a coarsely ribbed *Pavlovia* such as the form described here, lends more weight to the comparison between species which occur in the British *pallasioides* Zone and the Russian *pavlovi* Subzone.

Pavlovia sp. nov. aff. raricostata Ilovaisky, 1917

Plate 48, fig. 1

Material. One specimen (NMW 77.12G.84).

Horizon. Bed 2, Upper Kimmeridgian, basal rotunda Zone.

Description. The specimen is 80 mm in diameter with umbilical diameter of 30 mm. There are twenty-five primary and forty-four secondary ribs on outer whorl. Innermost whorls not well preserved but appear to have slender, fairly closely spaced ribs. Ribbing very rapidly becomes more widely spaced and at 20 mm diameter there are 21 ribs. At 25 mm diameter this has decreased to 19 ribs, and by 30 mm to 17. Ribs on last umbilical whorl become blunt and are rectiradiate or slightly rursiradiate. Point of furcation of ribs is just visible over last umbilical half-whorl, denoting slight uncoiling of umbilical seam.

Outer whorl ribs become yet more blunt and have wide angle of furcation. Occasional simple ribs interspersed with predominantly bifurcate ones; one polygyrate rib visible near mouth of shell. Rib density visibly increases over last half-whorl whose length is presumed to correspond to body-chamber. It is not known whether mouth of shell is peristome; it is devoid of any modification, but there is no trace of an umbilical seam beyond this point and thus it seems probable that little, if any, of the shell is missing.

Remarks. This specimen appears unique amongst material hitherto collected. Closest comparisons are with the Russian species *P. raricostata* (Ilovaisky's *P. iatrensis* var. *raricostata* emended Michailov 1962, p. 15) but there are important differences. Specimens of the latter species are smaller in diameter, even allowing for the crushing (see Michailov 1966, p. 56), and they do not have as many as twenty-five primary ribs on the last whorl. Inner whorl comparisons are, however, fairly close, and it is on this basis that affinity to *P. raricostata* is suggested. It is felt essential that further material is obtained before according this species a new name.

EXPLANATION OF PLATE 53

All figs. $\times 1$.

- Figs. 1, 4. Pavlovia pallasioides (Neaverson). NMW 77.12G.69, 77.12G.70. Bed 3e, 7.6 m below Bed 2.
- Figs. 2, 3. *Virgatopavlovia hounstoutensis* gen. et sp. nov. Holotype, NMW 77.12G.98, and paratype, 77.12G.99. 7.5 m below top of Rhynchonella and Lingula Beds.



Pavlovia sp. B

Text-fig. 8

Material. Two specimens (NMW 77.12G.49, 131).

Stratigraphical range. Upper Kimmeridgian, *rotunda* Zone, ranging from 1.0 to 1.85 m above Bed 2 (see below).

Description. The figured specimen (NMW 77.12G.49) has a diameter of 374 mm and an umbilical diameter of 153 mm; it has forty-five primary and at least seventy-five secondary ribs on its last whorl. At 60 mm diameter there are 27 ribs; at 70 mm, 29; 80 mm, 33; 90 mm, 38; 100 mm, 40; 110 mm, 43; 120 mm, 46; 130 mm, 46; 140 mm, 47; 150 mm, 49. Ribs of inner whorls straight, rectiradiate; tendency to become prorsiradiate on later whorls. Coiling is tight enough, and furcation point sufficiently high, to conceal branching of ribs on umbilical whorls.

Outer whorl ribs stouter, less sharp, fairly straight, mostly rectiradiate, but some prorsiradiate. Mainly bifurcate, but simple primary ribs quite common; few polygyrate ribs. Constrictions occur irregularly; present on all stages of the shell.

Specimen NMW 77.12G.49 does not show any marked uncoiling of the umbilical seam except over the last one-eighth of a whorl, nor does the crushing suggest the length (if any) of body-chamber present, so that it is not possible to tell if this specimen was mature. A trace of an umbilical seam continues for about 30 mm beyond the last preserved part of the shell, so that only a small part of it may be missing. Specimen NMW 77.12G.131 (not figured) is septate to at least 365 mm diameter. On this specimen a freak of preservation has allowed some sutures to be seen, and it is estimated from the umbilical seam trace over the last whorl of the shell, that its complete diameter must have been at least 430 mm. In other respects this specimen agrees well with the other, and it may thus be that the former is not as complete as appearances would suggest.

Remarks. The very large size of this specimen, the largest species of *Pavlovia* hitherto described, is a distinctive feature. The species is far more common than the collection of two specimens suggests; since the ammonites are very fragile, it needs the collection of specimens almost totally isolated from erosion to make a satisfactory cast, but such specimens are infrequently found.

In the soft grey clays 2.5 m below Bed 2, very large ammonites are frequently seen in section in the cliff. Specimens with a crushed diameter of up to 1.2 m were measured, though examination of the specimens proved impossible. It seems likely, though, that these specimens could be allied to *Pavlovia* sp. B.

P. kochi Spath (1936, p. 50, pl. 15, fig. 1) may be of a similar diameter, as the holotype is still septate at a diameter of 220 mm. The trace of the umbilical seam, however, suggests that the maximum uncrushed diameter was probably 270–280 mm. Even if specimens of *P. kochi* should prove to be of similar size to *Pavlovia* sp. B, the latter may be readily distinguished by the considerably coarser ribbing on the inner whorls; at diameters of around 60 mm there are about eight more ribs per whorl on *P. kochi*.

EXPLANATION OF PLATE 54

All figs. $\times 1$.

Fig. 1. Pavlovia aff. strajevskyi Ilovaisky. NMW 77.12G.85. Bed 3d, 9.0 m below Bed 2.

Figs. 2-4. *Virgatopavlovia fittoni* gen. et sp. nov. 2, holotype, NMW 77.12G.86, 7.5 m below top of Rhynchonella and Lingula Beds. 3, paratype, 77.12G.88. Typical fragmentary specimen, 4.5 m above specimen in fig. 2. 4, paratype, 77.12G.97. Horizon as in fig. 2.



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TEXT-FIG. 8. *Pavlovia* sp. B. NMW 77.12G.49, Bed 1, 1.85 m above Bed 2. $\times 0.48$.



TEXT-FIG. 9. Rib density of some Upper Kimmeridgian ammonites. D— Pectinatites (Pectinatites) dorsetensis; A—Pavlovia sp. A; S—P. superba; B—Pavlovia sp. B; W—P. composita waddingtoni.

Pavlovia rotunda (Sowerby, 1821)

Plate 47, fig. 2; Plate 51, fig. 2

1821 Ammonites rotundus Sowerby, p. 369, pl. 293, fig. 3.

1924 Pallasiceras rotundum (Sowerby) Spath, p. 16.

- 1925 Pallasiceras rotundum (Sowerby); Buckman, pl. 590.
- 1925 Pallasiceras rotundum (Sowerby); Neaverson, p. 18, pl. 1, fig. 6.
- 1931 Pavlovia rotunda (Sowerby) Spath, p. 431.
- 1933 Pavlovia rotunda (Sowerby); Arkell, pl. 40, fig. 6.
- 1947a Pavlovia rotunda (Sowerby); Arkell, pl. 5, fig. 1.
- 1956 Pavlovia rotunda (Sowerby); Arkell, pl. 41, fig. 5.

Material. Twenty-six reasonably whole specimens, large numbers of fragments of varying sizes.

Stratigraphical range. Upper Kimmeridgian, *rotunda* Zone, ranging from Bed 2 upwards to a point some 12 m above the Rotunda Nodule Bed (precise upper limit not determined).

Description. Neaverson's (1925) topotype is undoubtedly closely related to the holotype which is a waterworn fragment of body-chamber. The measurements given by Neaverson for this specimen are correct (1925, p. 18, pl. 1, fig. 6). At 15 mm diameter this specimen has 40 ribs; at 20 mm, 36; 25 mm, 31; 30 mm, 30; 35 mm, 29; 40 mm, 29; 45 mm, 28 (see range of rib densities in text-fig. 10). Last septum is at about 70 mm diameter and the body-chamber is 200° long. It is not possible to determine whether the peristome is preserved. Other specimens, though, appear to show the peristome at a similar diameter and one such specimen is figured here (Pl. 51, fig. 2). The peristome on this specimen is inflated both laterally and ventrally, suggesting that this could be a mature modification. This specimen is 102 mm in diameter, with a whorl height of 29 mm (28.5%), whorl thickness of 30 mm (29.5%), and an umbilical diameter of 50 mm (49.0%); thus the specimen is very close to Neaverson's topotype. Also figured here is a crushed specimen, typical of the forms found at horizons from Bed 2 up to the Rotunda Nodule Bed. This specimen (NMW 77.12G,121) is from 2.4 m above Bed 2. It is 130 mm in diameter (this dimension probably corresponds to an uncrushed diameter of 110 mm) and has an umbilical diameter of 54 mm. It is more coarsely ribbed than any of the topotypes; at 20 mm diameter this specimen has 28 ribs; at 25 mm, 24; 30 mm, 25; 35 mm, 25; 40 mm, 25; 45 mm, 26; 50 mm, 27. These rib densities are quite close to ones obtained from topotypes at diameters of over 30 mm; at smaller diameters the Rotunda Nodule Bed forms are more finely ribbed. From beds below the Rotunda Nodule Bed have been obtained specimens showing a fairly complete series of forms which link the specimen figured in Plate 47, fig. 2, with that figured in Plate 51, fig. 2, so that there is little doubt that both forms belong to the same species. The diameter of crushed forms varies from an estimated 100 mm to 130 mm and most of these seem to be mature forms and probably therefore directly comparable with Rotunda Nodule Bed forms.

Remarks. Ammonites have long been known from the calcareous nodule horizon which makes up the Rotunda Nodule Bed, but outside the nodules themselves at and around their horizon, specimens are frequently found which have been partially preserved in the round and partly crushed; the uncrushed portion may equally often be of body-chamber or of phragmocone. These uncrushed portions of ammonites are fairly resistant to marine erosion and partly rounded specimens may be found on the beach (particularly in the less accessible areas). It is to this category that Sowerby's holotype belongs; as stated earlier, it is a waterworn body-chamber fragment, and quite possibly came from the clays around the Nodule Bed horizon and not from the nodules themselves as earlier workers have surmised (Buckman, 1925, legend to pl. 590; Neaverson 1925, p. 19). There can be no doubt, however, that the horizon from which the holotype came was within 2 m of the Rotunda Nodule Bed.

Pavlovia rotunda gibbosa (Buckman, 1926)

Plate 50, fig. 3; Plate 51, fig. 3; Plate 52, fig. 2

- 1926 Lydistratites lyditicus Buckman, pl. 353C, D.
- 1926 Lydistratites gibbosus Buckman, pl. 639A-C.
- 1926 Lydistratites trigonalis Buckman, pl. 674A, в.
- 1927 Lydistratites gibbosus Buckman, pl. 639D.
- 1936 Pavlovia (Pallasiceras) gibbosus (Buckman) Spath, p. 27.
- 1936 Pavlovia (Pallasiceras) trigonalis (Buckman) Spath, p. 27.

Material. Seven specimens.

Stratigraphical range. Upper Kimmeridgian, rotunda Zone, occurring in the rotunda Nodule Bed (see Remarks).

Description. Specimen BM C.77954 (Pl. 51, fig. 3a, b) is very close in all characters to Buckman's *L. lyditicus* 'plesiotype'. It is entirely phragmocone, 97 mm in diameter, with a whorl height of 26 mm (27%), whorl

thickness of 38.5 mm (40%), and an umbilical diameter of 50 mm (52%). These figures compare closely with those quoted by Buckman, except that this specimen appears to have a more depressed whorl section. At 35 mm diameter there are 24 ribs; at 40 mm, 23; 45 mm, 23; 50 mm, 24. There are thirty-one primary and fifty-six secondary ribs on the last preserved whorl. Specimen BM C.74670 (Pl. 50, fig. 3) is more finely ribbed; at 20 mm diameter it has 41 ribs; at 25 mm, 36; 30 mm, 32; 35 mm, 28; 40 mm, 26; 45 mm, 25; 50 mm, 25.

Remarks. The holotype of *P. rotunda gibbosa* is a large phragmoconic whorl segment, but the proportions of the shell and Buckman's measurements (222, 28, 40, 50) agree closely in all respects except absolute size with those given above for specimen BM C.77954. Specimen BM C.74670 has a less depressed whorl section but is otherwise similar (148, 28, 34, 51).

This subspecies is separated from *P. rotunda* on the basis that *P. rotunda* is apparently mature at a diameter of around 100–120 mm (uncrushed). *P. rotunda gibbosa* is mature at an estimated 300–400 mm, and thus specimens of *P. rotunda gibbosa* are still entirely septate at around 100–120 mm. I consider, however, that the two forms are linked by similar rib style and density, but there appears to be a tendency towards a depressed whorl section in *P. rotunda gibbosa*. It is possible that *Pavlovia* sp. B is closely related to this subspecies but the information available suggests that the former is more finely ribbed. More material is clearly needed for the relationships of *P. rotunda gibbosa* to other pavloviids to be more readily apparent.

L. trigonalis Buckman seems to differ from L. gibbosa only in its whorl section; it appears probable that the triangular section may not be an original feature, but even if it were the differences do not appear sufficient to warrant specific distinction.

The association of the large phragmoconic fragments such as Buckman depicted (a further typical example is figured on Pl. 52, fig. 2) with the smaller specimens of inner whorls, is based on lack of maturity of these latter forms at diameters around 100 mm (or more), and agreement in shell proportions. In the case of the Rotunda Nodule Bed fauna, these are the only possible smaller forms which can be matched with the larger phragmoconic specimens. Once all the smaller mature forms have been eliminated from consideration, few specimens remain, and amongst those remaining it seems logical to unite forms which are mature at larger diameter than *P. rotunda s.s.*

Even larger phragmoconic fragments have been seen in collections from the Rotunda Nodule Bed. Adult diameter of such large forms must have been well over 400 mm and they may be related to the earlier *Pavlovia* sp. B (see p. 508), which is, however, somewhat more finely ribbed. There is some resemblance between *P. rotunda gibbosa* and the Greenland species *P. inflata* Spath (1936, p. 49, pl. 14, fig. 1a-c), even down to the constrictions visible throughout development. However, that species is more involute and has a yet more depressed whorl section.

Pavlovia concinna (Neaverson, 1925)

Plate 47, fig. 1; Plate 48, fig. 2; Plate 49, figs. 2, 3; Plate 50, fig. 2; Plate 51, figs. 1, 4; Plate 52, figs. 1, 3, 5

- 1925 Pallasiceras concinnum Neaverson, p. 19, pl. 1, fig. 7.
- 1925 Pallasiceras pringlei Neaverson, p. 20, pl. 1, fig. 10.
- 1925 Pallasiceras gracile Neaverson, p. 20, pl. 1, figs. 8, 9.
- 1936 Pavlovia (Pallasiceras) concinna (Neaverson) Spath, p. 42, pl. 10, fig. 2.

Material. Fifty-five specimens, including both crushed and uncrushed forms.

Stratigraphical range. Upper Kimmeridgian, *rotunda* Zone, ranging from Bed 2 upwards for about 13 m above the Rotunda Nodule Bed (precise upper limits of range not determined).

Description. Diameter of uncrushed specimens referable to this species varies from 38 to 58 mm, though in the case of some smaller diameter forms it is difficult to establish whether they are mature. Proportions of shell appear to remain fairly constant in spite of these size differences. Thus whorl height varies from 30 to 35% of diameter, whorl thickness from 31 to 34%, and umbilical diameter from 43 to 50% (the larger figure obtains on the larger diameter mature forms where noticeable uncoiling of the umbilical seam takes place).

Ribs on innermost whorls frequently scarcely discernible; in some specimens these whorls are virtually smooth, bearing only traces of prorsiradiate striations, and it is not until the antepenultimate whorl, at an umbilical diameter of 7–8 mm, that the ribs become readily apparent. Earliest ribs exceptionally densely arranged, low in profile, and very fine, in some cases difficult to accurately assess rib density. At 15 mm diameter the number of ribs varies between approximately 40 and 55, at 20 mm, 32–45, and at 25 mm (beyond the umbilical diameter in most specimens), 33–34. This variation in rib density is greater at small diameters than in the other species of *Pavlovia* described here, and may be in some measure dependent on the diameter at which the initial ribs were developed (i.e. the point at which the ribs are genuine ribs and not merely striations). There also seems to be a correlation between mature size and rib density; larger specimens have less dense ribbing at small diameters than those with a smaller mature diameter. This raises the possibility that ultimate size could have been a function of rate of growth.

Ribs on inner whorls fine and slender; initially rursiradiate at umbilical shoulder, then swing forwards sharply to become rectiradiate to markedly prorsiradiate though fairly straight throughout their course beyond the shoulder. Bifurcation points often quite low on whorl side and on some specimens are regularly only half way up the side. Regular intercalations of simple unbranched primary ribs occur on these early whorls, sometimes as frequently as every third rib.

The change from fine, densely packed ribs of the inner whorls to coarsely ribbed outer whorl is accomplished in less than half a whorl of rapidly coarsening ribs.

Body-chamber very variable in length, from one-third of a whorl to almost three-quarters, with most specimens about three-fifths of a whorl. Ornamentation of body-chamber consists of irregular strong bifurcating ribs, in some cases with occasional constrictions. As with other species of the genus these may be preceded by a polygyrate furcation and succeeded by a simple rib. In some cases such a simple rib is quite prominent ventrally, forming a flare-like feature.

The aperture is modified in some examples from the Rotunda Nodule Bed. In one (NMW 77.12G.117; Pl. 51, fig. 4), lateral extensions of the peristome are visible, although the specimen does not have its ventral portion preserved. Another specimen (NMW 77.12G.118; Pl. 51, fig. 1) shows a ventral extension of the peristome coupled with a thickening of the shell in a manner recalling the horn of the pectinatitids of lower horizons. The ventral extent of the projection is exaggerated by a calcite-filled vein running across it which has displaced it ventrally. On some other specimens (e.g. BM C.77944; Pl. 52, fig. 1) the ribs fade towards the peristome; the peristomal region is smooth, and there is a slight ventral and lateral inflation.

Crushed specimens from horizons both above and below the Rotunda Nodule Bed agree in character with the uncrushed forms on which the above description is primarily based. If allowance is made for the crushing they would all seem to fall within the range of diameters given above. The crushed diameters range from 50 to 66 mm; these figures probably represent original diameters of 42–57 mm. The specimens from Bed 2 appear to lie towards the coarser end of rib density variation as far as the inner whorls are concerned, and the transition from the fine ribbing of the inner whorls to the coarse ribbing of the outer whorl is a more gradual process in these earlier forms. This results in a smaller number of ribs on the outer whorl of specimens from Bed 2 (mean value of the number of primary ribs on the outer whorl of sixteen specimens of this species from Bed 2 is 24.2; mean value for twelve specimens from the Rotunda Nodule Bed is 25.8).

On the body-chamber the ribs are chiefly bifurcate but on most specimens there are examples of simple unbranched primary ribs and intercalatory secondaries. On one specimen (NMW 77.12G.55; Pl. 48, fig. 2) there is a single trifurcate rib about one-third of a whorl back from the peristome; this is not a polygyrate rib as it has only a single furcation point, and is one of the few *Pavlovia* specimens noted so far in the Dorset faunas to show this feature. Amongst the *Pavlovia* species figured by Ilovaisky (1917) this, however, seems to be a fairly common characteristic.

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Remarks. There are several discrepancies between the figures on Neaverson's 1925 plate 1 and the actual specimens. The paratype of *P. gracile* is 34 mm in diameter and not 42 mm as the 'natural size' plate suggests. This magnification gives a misleading idea of the specimen, which is in fact much more like the smaller variants of *P. concinna* which Neaverson described as *P. pringlei*. Neaverson's plate 1, fig. 8 (the holotype of his *P. gracile*) was stated by him to be, and is, 42 mm in diameter. The 'natural size' plate, however, shows an ammonite 49 mm in diameter. More important, however, Neaverson omitted to mention two features shown by this specimen: (1), that it is incomplete; and (2), that on the reverse side a section of the missing part of the shell is preserved; the complete shell would have been 53–54 mm in diameter. This latter specimen is therefore very closely comparable in size with the holotype of *P. concinna* (estimated diameter 53 mm). In other characters it is very similar too, and is probably as closely similar to the holotype of *P. concinna* as any two pavloviids are one to the other.

The specimen figured by Spath (1936, pl. 10, fig. 2; GSM 72216) was labelled on the plate as *P. rotunda* though the text (1936, p. 42) makes it clear that Spath figured the specimen as *P. concinua*. There was clearly an error in the labelling of the plate and the specimen belongs properly with *P. concinna*.

The small adult size of this species and the characteristic ornament are sufficiently distinctive features to render it readily recognizable in the field; there are no other described British species of *Pavlovia* with which it is likely to be confused. The closest similarities are with some of the small forms figured by Ilovaisky (1917; e.g. *P. modesta*, pl. 2, fig. 5), though none of these has the same combination of finely ribbed inner whorls and coarsely ribbed body-chamber at such a small diameter.

As *P. concinna* is undoubtedly a microconch species, it seems highly probable that it is the microconch of *P. rotunda*. It is noticeable that *P. concinna* is far more abundant than *P. rotunda* in Bed 2, but at other horizons both are commonly represented.

Genus VIRGATOPAVLOVIA gen. nov.

Type species. Virgatopavlovia fittoni sp. nov.

Diagnosis. Dimorphic. Macroconchs ribbed on inner whorls with sharp, fine, bifurcating ribs with high furcation point. Secondary ribs sharp, closely paired as in *Epipallasiceras*. Outer whorl with irregular ribbing frequently virgatotome, but also with polygyrate, bifurcate, or simple ribs and intercalatory secondaries. Body-chamber approximately half a whorl in length. Peristome simple. Microconchs ribbed similarly to macroconchs on inner whorls. Body-chamber with mainly bifurcate ribs as inner whorls, but occasional polygyrate and simple ribs. Peristome simple, frequently preceded by a virgatotome rib. Body-chamber three-eighths to one-half whorl long.

Stratigraphical range. Upper Kimmeridgian, fittoni Zone.

Remarks. Ammonites included in this new genus occur in the uppermost beds of the Kimmeridge Clay. They show the characteristic rib style on the inner whorls of the Greenland genus *Epipallasiceras*. Spath (1936, p. 29) proposed this name as a subgenus of *Pavlovia* for a series of Greenland forms which are characterized by sharp



TEXT-FIG. 10. Rib density of some Upper Kimmeridgian ammonites. R— Pavlovia rotunda; P—P. pallasioides; C—P. composita; F—Virgatopavlovia fittoni.

ribbing, a high bifurcation point with close pairing of the secondary ribs, and fairly wide rib interspaces. Most of the specimens figured by Spath were incomplete, but the holotype of *E. pseudaperta*, the type species (Spath 1936, p. 56, pl. 16, fig. 1), appears to be a macroconch. Other specimens he figured (e.g. 1936, pl. 9, fig. 3) could well be microconchs. I earlier identified incomplete ammonites from the higher horizons of Hounstout Cliff as species of *Epipallasiceras* (Cope 1971, p. 41), but when more complete material was collected showing outer whorls with strong, often virgatotome ribbing, it seemed unrealistic to relate such forms to *Epipallasiceras*. The presence of virgatotome ribs, or even more than the very rare polygyrate ribs, seems unknown in *Epipallasiceras*. The microconchs of *Virgatopavlovia*, too, often show virgatotome ribbing, sometimes restricted to a single rib immediately preceding the smooth, though well-defined, peristomal margin.

Equation of these Dorset ammonites with other known genera or subgenera also raises difficulties. There are undoubted similarities to species of *Zaraiskites* Semenov, 1898, which genus I earlier identified with some of these forms (Cope 1971, p. 41). This latter genus appears to contain two distinct species groups: (a) The group of *Z. scythicus* (Vischniakoff). These have finely ribbed inner whorls showing irregular furcation with simple, bifurcate, or polygyrate ribs. The outer whorls (or at least the body-chamber) have virgatotome ribs interspersed with irregular developments of simple, bifurcate, polygyrate, and polyploke ribs, the latter preceding constrictions. (b) The group of *Z. zarasjkensis* (Michalski), which appears intermediate between *Zaraiskites* of the *scythicus* group and *Virgatites*. In this group the furcation is virgatotome robs appear regularly disposed in sheaves of four to six, and only the very occasional simple rib interrupts this arrangement.

The Dorset forms appear similar to the species of the *scythicus* group of *Zaraiskites* in that the ribbing of the body-chamber is irregular but chiefly virgatotome. They differ, however, fundamentally in the character of the ribbing of the inner whorls which is like the rib style of *Epipallasiceras* as described above.

Various species of *Virgatites* Pavlow, 1892 also show some resemblance to *Virgato-pavlovia*. Thus *Virgatites pilicensis* (Michalski 1894, pl. 6, fig. 10) has an outer whorl very similar to some of the Dorset forms. The inner whorls of the Russian species, however, bear virgatotome ribs. The same is true of another Russian species, *V. sosia* (Michalski 1894, pl. 4, figs. 6, 7), another *virgatus* Zone form, at first sight closely similar to Dorset specimens.

On the one hand therefore, *Virgatopavlovia* is similar to *Epipallasiceras*, but differs in the body-chamber ornament of frequent virgatotome or sometimes polygyrate furcation—a character not seen in any of the Greenland material of *Epipallasiceras*. On the other hand, there are similarities to *Zaraiskites* of the *scythicus* group, and to *Virgatites* of the *sosia* and *pilicensis* types. *Zaraiskites* is not known from beds as young as this in Russia (see section on correlations, p. 530) and detailed comparison with *Virgatites* also rules out that genus as a suitable taxon for these new species. For these reasons *Virgatopavlovia* is proposed for these forms; the genus is included in the Pavloviinae, for whilst showing characters of the Virgatitinae its inner whorls betray its pavloviid ancestry. The fauna may well be a time equivalent of *Epipallasiceras* of the Greenland subprovince, and of *Virgatites* of the Russian subprovince.

The genus is quite distinct from the later genus *Progalbanites* Spath, 1936, now known to be distinct from *Zaraiskites*. This former genus has polygyrate ribbed inner whorls and a polygyrate or virgatotome outer whorl; it completely lacks the sharp, close-paired bifurcate secondaries of *Virgatopavlovia*, and seems always to be of much smaller size.

Virgatopavlovia fittoni sp. nov.

Plate 54, figs. 2, 3; Plate 55, figs. 1, 4

1958 *Zaraiskites* sp. House, p. 10. 1970 *Zaraiskites* sp. Cope, p. 41.

Diagnosis. Macroconch Virgatopavlovia 108-125 mm in diameter. At 20 mm diameter

approximately 36-40 ribs; at 25 mm, 34-39; 30 mm, 33-38; 35 mm, 32-35; 40 mm, 30-33; 45 mm, 31; 50 mm, 32. Ribs on inner whorls sharp, slender, prorsiradiate; bifurcation point high, secondaries closely paired with wider interspaces between primaries. Outer whorl with thicker, sharp ribs, initially bifurcate, rapidly becoming predominantly polygyrate or virgatotome with up to five secondary ribs to one primary, occasional simple and bifurcate ribs and intercalatory secondaries. Body-chamber one-half whorl long. Peristome simple.

Holotype, NMW 77.12G.86; Paratypes, NMW 77.12G.87-96, 111-114.

Material. Fifteen specimens and large numbers of fragmentary specimens of varying sizes.

Horizon. Holotype from 7.5 m below the base of Hounstout Clay at Pier Bottom. Figured paratypes are from this horizon and from Hounstout Cliff at 3.0 m below base of Hounstout Clay.

Stratigraphical range. Upper Kimmeridgian, *fittoni* Zone, ranging from 8.0 m below base of Hounstout Clay to 1.5 m below top of Hounstout Clay. The occurrence of the species in other sections is discussed in the section on zonal stratigraphy (p. 528).

Description. Holotype 108 mm in diameter with an umbilical diameter of 42 mm; there are twenty-nine primary and an estimated sixty-five to seventy secondary ribs on the last whorl. Diameter of other measurable specimens varies from 108 to 125 mm; umbilical diameter varies from 41 to 55 mm. These figures possibly include some immature forms.

Ribs of inner whorls fine, slender, rectiradiate to prorsiradiate. On some specimens ribs of innermost whorls appear to be initially rursiradiate, but it is probable that this feature is not original and is due to crushing of shell. At 20 mm diameter, the holotype has approximately 40 ribs; at 25 mm, 39; 30 mm, 38; 35 mm, 35; 40 mm, 33. These rib densities suggest that the holotype is towards the finer-ribbed end of variation within the species. The holotype is fairly involute and only on the last half whorl within the umbilicus is the point of furcation visible. In most specimens a pronounced uncoiling of the umbilical seam occurs there, which exposes the secondary ribs. Ribs appear to be entirely bifurcate at this point and the secondary ribs from each primary do not diverge sharply but maintain a close sub-parallel course. Thus between each pair of the closely grouped secondary ribs there is a comparatively wide rib interspace.

Outer whorl ornament initially of bifurcate ribs, but within a few ribs the first polygyrate furcations appear and ribs then become irregular polygyrate or virgatotome. The holotype shows a lowering of the point of furcation with predominantly polygyrate ribs and occasional virgatotome furcations. In addition to the polygyrate and virgatotome furcations (with up to five secondary ribs on some specimens) occasional simple and bifurcate ribs persist with some intercalatory secondary ribs. The outer whorl thus presents a rather untidy array of irregularly disposed rib styles, though some specimens show more regularity of ornament than others, and no two specimens are the same in their outer whorl ornament.

Differential crushing strongly suggests that the body-chamber is half a whorl in length, though on the holotype it may be a little shorter in (preserved) length. Peristome straight and shell ribbed right up to peristome margin. The holotype may not be a mature form. At first sight it is mature and appears to have a modified peristome. If, however, comparisons are made with other specimens, it may be seen that the size and ornament can be exactly matched by other specimens at the same diameter. Thus even the apparently modified peristome of the holotype can be matched with the paratype figured in Pl. 55, fig. 1 a quarter

EXPLANATION OF PLATE 55

All figs. $\times 1$.

Figs. 1, 4. *Virgatopavlovia fittoni* gen. et sp. nov. 1, paratype, NMW 77.12G.90, 7.5 m below top of Rhynchonella and Lingula Beds. 4, paratype, 77.12G.89, 4.5 m above specimen in fig. 1.

Fig. 2. *Epivirgatites* cf. *nikitini* (Michalski). Plasticine impression from external mould of inner whorls of specimen from 1.0 m above *Exogyra* Bed, Portland Sand, West Weare, Portland. Author's collection.

Fig. 3. *Epivirgatites nikitini* (Michalski). 1.0 m above *Exogyra* Bed, Portland Sand, West Weare, Portland. Author's collection.



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of a whorl back from its peristome; at this point, this paratype is 107 mm in diameter and has an umbilical diameter of 42 mm—measurements corresponding more or less exactly to those of the holotype and strongly suggesting that the holotype is immature or that about one-quarter of a whorl is missing.

Remarks. This species is one of the most common forms in the higher beds of Hounstout Cliff, in certain very restricted horizons separated by greater thicknesses of virtually barren rock. Usually the fossils are very poorly preserved and often fragmentary, they crumble readily unless excavation is made deeper into the less weathered parts of the clays. This is clearly the reason that this species has not been found hitherto. The 'triplicate forms' referred to by Spath (1936, p. 161) are from these beds and included fragments probably belonging to this species. In the Spath collection are a small number of very poorly preserved ammonites from Pier Bottom, quite clearly from the same horizon as that which yielded the holotype of *V. fittoni*.

The specimen from Portland recorded by House (1958, p. 10) is in the Sedgwick Museum, Cambridge (J47127a). It had been identified as *Zaraiskites* cf. *scythicus* by Arkell, according to the label. Examination of the specimen leaves no doubt that it is a typical *V. fittoni*; the outer whorl of the specimen has been damaged during growth and the body-chamber shows rather atypical ornament at this point. The specimen came from 4 m below the Black Nore Sandstone on Portland Isle, a horizon from which I have also collected the species. This occurrence provides a firm basis for correlation between the Portland and Purbeck areas near the Kimmeridgian–Portlandian boundary and confirms an earlier surmise by Arkell (1947*a*, p. 120).

Virgatopavlovia hounstoutensis sp. nov.

Plate 53, figs. 2, 3; Plate 54, fig. 4

1971 Epipallasiceras sp. Cope, p. 41.

Diagnosis. Microconch *Virgatopavlovia* 70–80 mm in diameter. Approximate rib density at 15 mm, 33 ribs; at 20 mm, 31; 25 mm, 31; 30 mm, 32. Ribs on inner whorls sharp, slender prorsiradiate. On outer whorl sharp with close-paired secondaries as *Epipallasiceras* but with variable number of polygyrate ribs. Peristome simple, preceded by a virgatotome or polygyrate rib. Body-chamber one-half to three-fifths of a whorl long.

Holotype. NMW 77.12G.98; Paratypes, NMW 77.12G.97, 99-105.

Material. Nine reasonably complete specimens, many fragments of various sizes.

Horizon. Holotype from 7.5 m below base of Hounstout Clay on Hounstout.

Stratigraphical range. Upper Kimmeridgian, fittoni Zone, ranging from 8 m below base of Hounstout Clay to 4 m below the Massive Bed.

Description. Diameter of measurable specimens varies from 70 to 80 mm. Holotype 73 mm in diameter with umbilical diameter of 29 mm. There are twenty-seven primary and an estimated fifty-three secondary ribs on the last whorl of the holotype. Rib density as in Diagnosis (above). Ribs of innermost whorls are fine, slender, with tendency to gentle prorsiradiate curve. On last umbilical whorl ribs become markedly prorsiradiate, fairly straight; where umbilical seam of outer whorl uncoils, point of bifurcation is visible. Secondary ribs arise with very acute angle of furcation, thus pairs of ribs are separated by comparatively wide rib interspaces. This feature is very noticeable on the outer whorl where ribs are predominantly bifurcate, but interspersed irregularly amongst these are polygyrate and simple ribs. Peristome preceded in

virtually every specimen by a polygyrate or virgatotome rib. Peristome smooth, fairly straight, ornamented solely by growth lines.

Some specimens show shallow constrictions on the body-chamber. The degree of crushing does not, however, allow this to be determined definitely, but the association of a polygyrate rib with a very low initial furcation followed by a simple rib suggests a constriction at these points. Differential crushing suggests that the body-chamber is one-half to three-fifths of a whorl in length.

Remarks. The similarity of *V. hounstoutensis* to species of *Epipallasiceras* has been discussed above (p. 516). I have no doubt that the former is a microconch species of *Virgatopavlovia* and may well be the microconch of *V. fittoni.* This association argues convincingly that *V. hounstoutensis* is not an *Epipallasiceras* and this possibility must therefore be precluded. It remains true, however, that fragments of the species can be confused with *Epipallasiceras* and one such specimen is figured here (Pl. 56, fig. 2) to show this similarity. The possibility remains that this is an *Epipallasiceras*, but the fact that more complete material can be seen to be quite distinct suggests that this is not all that likely.

The specimen figured by Buckman (1926, pl. 693) as *Virgatites pallasianus* has a lower furcation point than the specimens here referred to *Virgatopavlovia*. It appears to resemble *Epipallasiceras* more closely than it does *Virgatopavlovia*. This specimen was from the Massive Bed of Purbeck, only a little higher in the succession but at the base of the succeeding *albani* Zone.

Virgatopavlovia sp. nov. aff. fittoni

Plate 56, fig. 1

Material. Two fairly complete specimens (NMW 77.12G.108, 109), several fragments.

Stratigraphical range. Upper Kimmeridgian, fittoni Zone, ranging from 7.5 m below base of Hounstout Clay to 4 m below the Massive Bed.

Description. The figured specimen (NMW 77.12G.108) has a diameter of 178 mm and an umbilical diameter of 70 mm. At 50 mm diameter there are about 26 ribs; at 60 mm, 28; 70 mm, 28. Ribs on inner whorls are quite sharp, and visible furcations within umbilicus show close bunching of each pair of secondary ribs. Outer whorl primary ribs more rounded in cross-section and stronger; mainly virgatotome and polygyrate, furcation point very low on whorl side. Some bifurcate and simple ribs and intercalatory secondaries.

Peristome not preserved on any specimen and length of body-chamber not known, but crushing suggests there is about three-fifths of a whorl of body-chamber on the figured specimen, and this is therefore a minimum length.

Remarks. This species bears some resemblance in rib style to *V. fittoni*. It differs, however, in its greater mature size, the blunt nature of the ribs on the body-chamber, and is probably coarser ribbed on the inner whorls. Large, indeterminate fragments common in the topmost beds of the Kimmeridge Clay on Hounstout may belong to this species.

CLASSIFICATION OF THE UPPER KIMMERIDGIAN AMMONITES

The suprageneric classification of uppermost Jurassic perisphinctid ammonites is fraught with problems. At this time separation of the faunal provinces reached its maximum and separate ammonite stocks flourished in each province. The British area is within the Boreal faunal province of Kimmeridgian and Portlandian times, but within this province, different faunas can be recognized in particular areas. For example, differences exist between the faunas of Britain and Greenland, and each of these areas has different faunas from the Russian ones, with the development of local genera of very restricted areal distribution.

The problem becomes more pronounced when it is recognized that the phenomenon of heterochronous homoeomorphy could also be present. As further material is studied, so further examples of homoeomorphy amongst these late Jurassic perisphinctid ammonites have come to light. Thus, work on the lower part of the Upper Kimmeridgian was confused for many years because it was believed that the British early Upper Kimmeridgian faunas were to be correlated with those of the Lower Tithonian of Germany; it is only fairly recently that these correlations have been shown to be erroneous (Cope 1967) and to be based on correlations between two quite separate, but largely homoeomorphic, stocks.

Arkell (1957) placed the late Jurassic perisphinctid ammonites of the Boreal province in three subfamilies of the family Perisphinctidae. These were the Virgatosphinctinae Spath, 1924, the Dorsoplanitinae Arkell, 1950, and the Virgatitinae Spath, 1924.

Amongst the forms included in the Virgatosphinctinae is the genus *Pectinatites*. I previously demonstrated that this form can be traced back to the earlier *Propectinatites* (Cope 1968a), thus carrying the lineage nearer to its presumed origin in Upper Oxfordian/Lower Kimmeridgian ataxioceratids. Many Virgatosphinctinae possess the polygyrate rib style as a feature at least at some point of their development, and thus they all have presumably an origin in the ataxioceratids where this rib style originated (Geyer 1961). As these forms have this common ancestry they can conveniently be placed in a single subfamily, albeit large. The Virgatosphinctinae are thus a subfamily containing a wide variety of ammonites embracing many shell shapes and forms and of cosmopolitan spread. The *Pectinatites* group were separated by Zeiss (1968) as a tribe of the Virgatosphinctinae (the *Pectinatitini*); to me the *Pectinatites* group seem to be a purely Boreal series of genera of the Virgatosphinctinae, but the fact that they are Boreal is in itself no valid reason for separating them from other forms.

The Dorsoplanitinae of Arkell (1957) are an exclusively Boreal subfamily and include all post-*pectinatus* Zone perisphinctids of the British Kimmeridgian and Portlandian with the exception of the Virgatitinae. The Dorsoplanitinae of Arkell seem to me to include two distinct and usually readily separable groups of which one, the Pavloviinae, is considerably larger than the other.

The Pavloviinae (*pro* Pavlovidae Spath, 1931; Pavlovinae Spath, 1936) are a remarkably homogeneous group; they are clearly derived from the Virgatosphinctinae via *Pectinatites* (see p. 489) and not from *Subdichotonuoceras* as formerly believed (Arkell 1957, p. L332). The subfamily includes most of the Upper Kimmeridgian and Portlandian ammonites, many of them barely distinguishable from *Pavlovia* itself, and includes the 'Portlandian giants'.

The Dorsoplanitinae would then be a much more restricted subfamily and would include forms like *Dorsoplanites* itself and its descendant *Laugeites*, these perhaps leading on to the craspeditids in later Portlandian times. The origin of the dorsoplanitids could have been via the *Sphinctoceras/Subdichotomoceras* group, which already in *wheatleyensis* Zone times shows very prominent ribs with multiple secondaries tending to obsolescence, but some species of *Pectinatites* (particularly those included by Buckman in his genus *Wheatleyites*) show this tendency in the *pectinatus* Zone. The only known British *Dorsoplanites* occur in the *pallasioides* Zone (of the Midlands), and already by this time the genus is quite distinct (see Neaverson 1925, pl. 1, fig. 11). Spath (1936, p. 28) stated that Greenland specimens supported the common origin of *Pavlovia* and *Dorsoplanites*, and figured 'transitional' forms between the two genera (e.g. 1936, pl. 26, fig. 3). This argues for a close relationship between the two forms, and this is a good example of a form apparently intermediate between two separate subfamilies.

The subfamily Virgatitinae was stated by Arkell (1957, p. L334) to include 'extreme developments of either Virgatosphinctinae or Dorsoplanitinae, or both'. The greatest development of virgatotome ribs occurs in the genera *Virgatites* and *Zaraiskites*, but Arkell also included in this subfamily the genus *Michalskia* which has few such ribs. If the presence of virgatotome ribs is the criterion for placing an ammonite in this subfamily, then it must also include *Epivirgatites*, *Progalbanites*, and *Virgatopavlovia* gen. nov. However,

EXPLANATION OF PLATE 56

Both figs. $\times 1$.

- Fig. 1. Virgatopavlovia sp. nov. aff. fittoni. NMW 77.12G.108, 7.5 m below top of Rhynchonella and Lingula Beds.
- Fig. 2. V. cf. hounstoutensis. NMW 77.12G.107. Typical fragmentary specimen showing similarity of incomplete material to *Epipallasiceras*. 7.5 m below top of Rhynchonella and Lingula Beds.



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some later genera and species show virgatotome ribbing. For example, specimens of *Crendonites gorei* (Salfeld) collected from the top of the Portland Sand display virgatotome furcations on the innermost whorls. Higher still, in the Portland Stone, '*Galbanites' fasciger* Buckman shows the same feature, but the adult of which it is the nucleus, *Titanites polymeles* (Buckman), looks a typical giant pavloviid, and moreover is associated at the same horizon with other large pavloviids which have bifurcate inner whorls and no trace of virgatotome ribs.

In other words the presence of virgatotome ribs, in itself, is not sufficient to warrant the inclusion of a genus in the Virgatitinae. Other factors must be taken into account, and the possible ancestry of a particular form is clearly a factor which must have overriding priority.

In the case of *Virgatopavlovia* there is an immediate problem in that it is cryptogenetic; it is known so far only from Dorset, and the beds below do not yield (or have not yet yielded) a satisfactory ancestral form. Classification in this case depends upon whether one looks on *Virgatopavlovia* as displaying evidence of palingenesis or of proterogenesis. If the former, an origin in the Pavloviinae is called for. If the latter, the inner whorls could be taken to presage *Epipallasiceras*, whilst the body-chamber could support an origin in the Virgatitinae; but this would have the effect of separating *Epipallasiceras* completely from *Pavlovia*, to which it is seemingly closely related.

These sorts of arguments could of course make nonsense of any classification, and in a group in which there is so often some degree of homoeomorphy, it seems best to retain a conservative though flexible classification, and it is quite possible under such a scheme to place some genera into either one of two (or more) subfamilies. This was a conclusion reached by Spath (1933, p. 688) who wrote 'the fact that a given form may equally well be accommodated in genera that are referred to distinct families need not inconvenience those who look upon palaeontological nomenclature as a (very inadequate) servant and, above all, do not allow it to become a bad master'. Although Spath was here referring to the placing of species into genera, the same considerations surely apply at a higher taxonomic level.

THE AMMONITE ZONES

Earlier collections from the upper part of the Kimmeridge Clay of Dorset, of which the Spath and Waddington collections are the two most noteworthy, consist predominantly of ammonites from those horizons from which they can be readily collected. These horizons include the Rotunda Nodule Bed, and Blake's Bed 2. The ammonites from the soft clay and mudstone horizons which make up the bulk of the Kimmeridge succession are barely represented in these earlier collections. It is thus not surprising that the new collections, on which these descriptions are based, have for the first time established the horizon at which species first described from the south Midlands occur. The results are a reflection of the condensed sequences characteristic of the south Midlands area, the scattered nature of the exposures (most of them now completely obliterated) and the lack of accuracy in the recording of horizons from which specimens were obtained in the past.

Casey (1967) concluded that the *pallasioides* and *rotunda* Zones had been listed in the wrong order by Neaverson (1924, 1925). Proof of this assertion can now be demonstrated in Dorset. The beds in Dorset, formerly assigned to the *pallasioides* Zone, are now placed in a new Zone, the *fittoni* Zone, whilst the *pallasioides* Zone fauna has been found beneath the *rotunda* Zone fauna.

TEXT-FIG. 11. Ranges of ammonite species within the upper part of the Upper Kimmeridge Clay in Dorset. 1, *Virgatopavlovia* sp. nov. aff. *fittoni*. 2, *V. hounstoutensis*. 3, *V. fittoni*. 4, *Pavlovia rotunda*. 5, *P. concinna*. 6, *P. rotunda gibbosa*. 7, *Pavlovia* sp. B. 8, *P.* aff. *raricostata*. 9, *Pectinatites (Pectinatites) circumligatus*. 10, *Pavlovia pallasioides*. 11, *P. composita waddingtoni*. 12, *P. composita*. 13, *P. superba*. 14, *P.* aff. *strajevskyi*. 15, *Pectinatites (Pectinatites) devillei*. 16, *Pavlovia* spp. indet. 17, *Pavlovia* sp. A. 18, *Pectinatites (Pectinatites) dorsetensis*. 19, *P. (P.) strahani*. 20, *P. (P.) tricostulatus*. 21, *P. (P.)* cf. *pectinatus*. 22, *P. (P.) cornutifer*.¹ 23, *P. (P.) naso*.² 24, *P. (P.) paravirgatus*.² 25, *P. (P.) rarescens*.

¹ See also Cope 1967.

² See Cope 1967 for description.

Note also that Pavlovia spp. indet. range through the fittoni Zone.

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Pectinatites (Pectinatites) pectinatus Zone

The ammonite faunas of the lower part of this zone have been described in my earlier work on the Upper Kimmeridge Clay (Cope 1967). As a result of work on these faunas over other areas of Britain (Callomon and Cope 1971; Cope 1974*a*, *b*), the lower part of the zone is now distinguished as the *eastlecottensis* Subzone, and the upper part as the *paravirgatus* Subzone. In Purbeck the *eastlecottensis* Subzone embraces a thickness of 19·15 m from the White Stone Band up to the top of Blake's Bed 11. The faunas of that subzone have been detailed earlier, as the lower part of the *pectinatus* Zone (Cope 1967, pp. 7, 70) and are thus not dealt with in detail here.

Pectinatites (*Pectinatites*) *paravirgatus* Subzone. The *paravirgatus* Subzone includes horizons from the base of the Freshwater Steps Stone Band (Blake's Bed 10) up to the top of Blake's Bed 5, a thickness of 19·2 m (coincidentally virtually identical to the thickness of the *eastlecottensis* Subzone here).

Only one specimen of the subzonal index species has yet been recorded (Cope 1967, p. 63), but allied species (e.g. *P.* (*P.*) dorsetensis) occur quite commonly in this subzone. In addition, pectinatitids included by Buckman in the genus Wheatleyites appear particularly characteristic. Thus *P.* (*P.*) rarescens and *P.* (*P.*) tricostulatus are both recorded from the subzone in Dorset. The fauna is an assemblage well known from the south Midlands where, unfortunately, the combination of a series of thin and condensed successions with previous imprecise recording of faunal horizons sometimes suggests that the eastlecottensis and paravirgatus faunas coexisted. However, study of borehole faunas through the basal part of the pectinatus Zone and discriminatory readings of faunal lists leave no doubt that the faunas of the two subzones are readily separable and recognizable (Cope 1974a).

Pavlovia pallasioides Zone

The *pallasioides* Zone includes Blake's Beds 3 and 4 of the Isle of Purbeck succession, having a total thickness of 34.8 m. These beds have previously been included in the *rotunda* Zone, following Neaverson (1924, 1925), and Arkell (1947*a*, p. 79) stated that 'Specific determination of the ammonites is impossible owing to the bad state of preservation'. Casey (1967, p. 130) suggested that the *pallasioides* Zone fauna occurred within the Crushed Ammonoid Shales (Beds 3 and 4).

The zone is now recorded for the first time in the Dorset succession. The Hartwell Clay at Aylesbury is the type locality for the *pallasioides* Zone, and descriptions of the fauna are to be found in Neaverson's 1925 paper. Further ammonites from the Hartwell Clay were figured by Spath (1936). The stratigraphical position of the Hartwell Clay was the subject of lively controversy for some considerable time, and illustrates well the difficulties which may occur when attempting to piece together a succession from a series of small and isolated exposures. This earlier controversy centred around Buckman's contention that the Hartwell Clay fauna was earlier than the *pectinatus* Zone. This was finally resolved when it was found that Buckman had been deceived about the provenance of some ammonites by a dishonest workman. Neaverson's placing of the *rotunda* Zone beneath the *pallasioides* Zone was accepted more or less without question, until Casey argued on evidence from the south Midlands that the *pallasioides* Zone was earlier (1967, p. 130).

In 1972 I had the opportunity of examining a temporary section of the Hartwell Clay in Aylesbury. The top of the section was marked by the Upper Lydite Bed. *P. pallasioides* seems a particularly appropriate choice as a zonal index species, for not only is it common in the type area, but also occurs in Dorset and has been recorded from Swindon (Kitchin 1926).

In Dorset, species (other than *P. pallasioides*) which are common in the Aylesbury area appear to be absent from the fauna, although it is possible that collection failure is responsible for this apparent absence; but a feature which appears to characterize Upper Kimmeridgian faunas at several horizons is that species which occur commonly in the south Midlands are often rare or even absent on the south coast. For example *Dorsoplanites ultimus* (Neaverson) has not been found south of the Aylesbury region; neither has the genus *Sphinctoceras* been found to the south of the Oxford area, lower in the succession. Within the Boreal faunal province, there seems to have been extreme provincialization of the faunas at this time, and differences between the Midlands and the south coast seem no longer unexpected.

P. pallasioides itself occurs from 10.0 to 6.5 m below Bed 2, and the apparent restriction of this species to some 3.5 m of clays suggests that the Hartwell Clay fauna is only equivalent to part of the thickness of beds included here in the *pallasioides* Zone. The earliest *Pavlovia* faunas of Dorset are apparently unrepresented in the Hartwell Clay and these lower beds of the *pallasioides* Zone are to be correlated with

the non-sequence reflected in the Lower Lydite Bed of the south Midlands. At present I consider that insufficient is known of these lower *pallasioides* Zone faunas to merit the recognition of a separate subzonal fauna, though this may prove desirable in the future.

A link with the *pectinatus* Zone below is provided by the occasional specimens of the genus *Pectinatites*, the youngest known species of which (*P. circumligatus*) occurs near the top of the zone. The base of the *rotunda* Zone above is marked by the appearance of the small pavloviids of the *concinna* group.

Pavlovia rotunda Zone

This zone includes beds from the base of Bed 2 up to a point 8.0 m below the base of the Hounstout Clay, comprising a thickness of 35.8 m.

The zonal index species is a characteristic fossil of all but the top 14 m of the zone, but the small microconch forms, such as *P. concinna*, with their relatively coarsely ribbed body-chambers are more readily recognized in the field; they appear first in the Kimmeridge section in Blake's Bed 2 which forms a very conspicuous datum on the beach at Chapman's Pool. The base of this bed is therefore taken as the base of the *rotunda* Zone in the Purbeck area. Small microconchs of this *concinna* group are common for some distance above the Rotunda Nodule Bed; they seem to persist for at least 13 m above this latter horizon, although the precise point in the section where they cease to occur is not easy to ascertain, as this is about the only part of the whole succession which is not readily accessible at some point. The basal part of the *Lingula* Shales has proved singularly poor in ammonites, but it seems that by this time the *concinna* group of pavloviids had become extinct. However, it is not until a point 8.0 m below the base of the Hounstout Clay that a recognizably new fauna with *Virgatopavlovia* appears.

Ammonites of the *concinna* group are amongst the most readily recognizable of the phosphatized forms found in the Upper Lydite Bed of the south Midlands, and this latter horizon was correlated by Casey (1967) with the Rotunda Nodule Bed of Chapman's Pool, thus vindicating an earlier correlation of Buckman's (1926, p. 31) which was not until very recently accepted. The pause in deposition, so marked further north, was probably minimal at Chapman's Pool, which evidently lay well away from the fringes of the depositional basin, although even here occasional ammonites may be partially phosphatized. Only a short distance to the west, at Ringstead Bay there is a typical Lydite Bed development at this horizon (Arkell 1947*a*, p. 82).

Virgatopavlovia fittoni Zone

This new zone is proposed for the beds above the *rotunda* Zone and includes horizons up to the base of the Massive Bed, marking the base of the Portland Sand in the succession on Hounstout Cliff. This latter horizon also marks the base of the *Progalbanites albani* Zone and the base of the Portlandian Stage. The junction with the underlying *rotunda* Zone is drawn at the first appearance of *Virgatopavlovia* at a point 8 m below the Hounstout Clay. The total thickness of rocks assigned to the zone is 37.35 m on Hounstout Cliff.

These beds have for many years been correlated with the *pallasioides* Zone, following Neaverson (1924, 1925), although Arkell (1947a, p. 79) stated that '... their association with the *pallasioides* Zone ... is still only tentative'. Earlier attempts to find identifiable ammonites were not successful although the Spath collection does contain a few fragmentary specimens which Spath concluded did not look like Hartwell Clay forms (Spath 1936, p. 161). The Waddington collection contains no significant material from these horizons.

The beds which constitute the *fittoni* Zone on Hounstout are characterized by increasing amounts of silt at some horizons. This feature and the prevalence of relatively large thicknesses of thickly bedded, poorly jointed clays, suggests that this was a period of fairly rapid sediment accumulation. The scarcity of bituminous horizons (apart from a few thin ones in the Hounstout Clay) may be another pointer in this direction. The horizons at which ammonites are found are quite discrete levels, separated by virtually barren sediments. Thus it seems that rapid sedimentation was interspersed with short periods of relatively slow deposition, during which ammonite shells accumulated in larger numbers.

The zonal index species is associated with other species of *Virgatopavlovia* and with occasional small pavloviids. These latter forms are seemingly devoid of the coarse-ribbed body-chamber so typical of the earlier *concinna* group, but no really adequate material has yet been obtained. Preservation of the whole fauna is almost always poor, and excavation for some distance under the surface is necessary to obtain

even remotely satisfactory material. Insufficient material has yet been collected to draw any firm conclusions on the range of the species of *Virgatopavlovia* within the zone.

Specimens of *Virgatopavlovia* have been found on Portland Isle in the Lower Black Nore Beds (Arkell 1947a, p. 120), where they were first recorded by House (1958, p. 10) as *Zaraiskites*. There, they underly a fauna with *Progalbanites* and succeed shales with poorly preserved *Pavlovia* spp. At Dungy Head, 1 km to the west of Lulworth Cove, a nodular horizon at the top of Arkell's Bed 3 (1935, p. 321) yielded a readily recognizable specimen of *V. fittoni*. Here, too, *Progalbanites* was found to occur a little higher in the succession, signifying the *albani* Zone above.

The fauna of this zone is thus distinctive and readily recognizable and is here recorded from three separate localities in Dorset, a distance of some 30 km separating the Portland from the east Purbeck sections. In inland localities, however, the zone has not been identified and it thus appears that it is missing at the non-sequence at the horizon of the Upper Lydite Bed in the south Midlands. Horizons at the critical level are not exposed in the Vale of Wardour, but around Swindon the underlying *rotunda* Zone is reduced to derived material in the Upper Lydite Bed and the Portlandian faunas rest directly on the *pallasioides* Zone.

CORRELATIONS

Great Britain

Northwards from the fine coastal sections of Dorset, information on the Kimmeridge Clay has almost entirely to be obtained from published records, for most of the inland exposures have long since vanished. A few recent boreholes have helped to confirm the faunal succession established on the coast (Callomon and Cope 1971; Cope 1974*a*).

Over much of the country, horizons younger than the *pectinatus* Zone are not preserved. In Yorkshire (Cope 1974b) the *eastlecottensis* Subzone is overlain by the Coprolite Bed at the base of the Speeton Clay, and this former horizon directly underlies the Spilsby Sandstone and Sandringham Sands further to the south in the Wash area (Cope 1974a).

It is only in the south Midlands from the Aylesbury region westwards to Swindon that higher horizons in the Kimmeridgian are known. This area has yielded many finely preserved ammonites at several horizons. The beautifully preserved irridescent ammonites of the Hartwell Clay of Aylesbury have long been known, and fine ammonites have also been obtained from the Shotover Grit Sands. The old brick and sand pits of the area were the source of most of the type material figured by Buckman and Neaverson. Unfortunately, the area also provided the basis for the zonal stratigraphy of the Upper Kimmeridgian and this resulted in an unsatisfactory zonal scheme which it has taken many years to untangle. In contrast, the type section in Dorset which was almost entirely ignored because of the badly preserved faunas appears to be entirely without breaks and has thus highlighted the non-sequences to the north (text-fig. 12).

The succession at Swindon, modified from Arkell (1947b, p. 118), Buckman (1923, p. 29), and Chatwin and Pringle (1922, p. 163) is:

	n	netres
Glauconitic Beds		1.0
Upper Lydite Bed	up to	0.15
Swindon Clay	up to	6.0
Lower Lydite Bed		0.2
Exogyra nana Beds	up to	1.2
Pectinatus Sandstone	up to	1.2

The *Pectinatus* Sandstone clearly belongs to the *eastlecottensis* Subzone of the *pectinatus* Zone, as it yielded the holotype of *P. (P.) eastlecottensis* (Salfeld). The overlying *Exogyra nana* Beds have yielded '*Perisphinctes* cf. *devillei*' (Buckman 1923, p. 29) which presumably refers to a *Pectinatites* microconch, and this may be representative of part of the *paravirgatus* Subzone. The latter subzone is largely reflected, however, in the non-sequence of the Lower Lydite Bed; this non-sequence must also take in the lower part of the *pallasioides* Zone. The Swindon Clay is to be correlated with the rest of the *pallasioides* Zone as it has provided *Pavlovia pallasioides* Zone ammonites (Kitchin 1926).

A major non-sequence is indicated by the Upper Lydite Bed, for the succeeding Glauconitic Beds yield ammonites characteristic of the top of the Portland Sand of Dorset. The Upper Lydite Bed therefore

	ZONES		KIMMERIDGE	SWINDON		OXFORD	
Zones o alboni Zo	f Portland Sond me at bose	~	PORTLAND SAND 39 m Massive Bed at base)	GLAUCONITIC BEDS Upper Lydite Bed		GLAUCONITIC BEDS 1.0m Upper Lydite Bed 0.3m	
VIR	G A TOPAV LOVIA		HOUNSTOUT MARL 21-00	E			
	FITTON		HOUNSTOUT CLAY 8-35 RHYNCHONELLA 8-00			MA	
	PAVLOVIA		LINGULA BEDS 15-00 ROTUNDA SHALES 13-50 ROTUNDA NODULE BED 1-80		ш U Z	S C C C C C C C C C C C C C C C C C C C	
	ROTUNDA	uctt)	SHALES 4-25 BED 2 1-25	EE			
	PAVLOVIA AILASIODES	ма дэнгия ма дэнгия о) сэланг	SHALES and CLAY 30.0m	S WINDON CLAY up to 6.0 m Lower Lydite Bed		WHEATLEY SANDS up to 36 m H A R T W ELL CLAY up to 3.6 m	7 1
		2		NO N - SEOUE N			
ATITES IATUS	PARAVIRGATUS SUBZONE	3 0	SHALES ond CLAYS ith some nodule horizons HWATED STEDS STONE BAND	19:20m Exogyro nano BED uptol:2	S E	SHOTOVER GRIT SANDS 4.5m	
PECTIN	A STLECOTTENSIS SUBZONE	> 5	SHALES with Middle Vhite Bond in middle VHITE STONE BAND	PECTINATUS SANDS	510NE	SHOTOVER FINE SANDS 1-2m	
HUDLESTO	NI ZONE BELOM	Q	CEY CLAYS ond SHAL	ES ? NON - SEOUEN	1 C E	? NON − SEOUENCE	
TEXT-F	IG. 12. Suggested correl	ation (of the upper part of the Up	per Kimmeridgian of Dorset	with the suce	cessions in the south Midlands.	

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embraces horizons from the basal *rotunda* Zone through the succeeding *fittoni* Zone and the lower zones of the Portlandian Stage.

The succession in the Oxford area shows marked similarities to that of the Swindon region, but there are some significant differences. The succession for the Oxford area listed below is modified from Arkell (1947*b*, pp. 107-110):

	r	netres	
Glauconitic Beds		1.0	
Upper Lydite Bed	up to	0.3	
Wheatley Sand*	up to	3.6	
Hartwell Clay	up to	3.6	
Lower Lydite Bed	up to	0.15	
Shotover Grit Sands		4.5	
Shotover Fine Sands		1.2	

* The Wheatley Sand listed here is the Wheatley Sand of Arkell (1947b), which is the Thame Sands of Arkell (1943). These are not to be confused with the Wheatley Sands of Buckman (1922, p. 28), or the Thame Sands of Buckman (1926, p. 36), which are both equivalent to the Shotover Grit Sands (see Arkell 1947b, pp. 110-111).

The Shotover Grit Sands have yielded a large ammonite fauna mainly indicative of the *paravirgatus* Subzone of the *pectinatus* Zone, but with possible representatives of the *eastlecottensis* Subzone. It seems more likely, however, that the Shotover Fine Sands are of *eastlecottensis* Subzone age and not of *hudlestoni* Zone age as I earlier suggested they might be (1967, p. 72). The Lower Lydite Bed probably encompasses a smaller non-sequence here than at Swindon and, in view of the fact that there is a good *paravirgatus* Subzone fauna below, may span only the lower *pallasioides* Zone.

The *pallasioides* Zone is represented in part by the Hartwell Clay, but the succeeding Wheatley Sand, which has not yielded ammonites, probably also correlates with this zone, since the Hartwell Clay is thinner here than at Swindon (where it is known as the Swindon Clay) and thinner too than its development at Aylesbury. The Wheatley Sand may thus be an arenaceous development of the upper part of the Hartwell Clay.

As at Swindon, the Upper Lydite Bed encompasses a major non-sequence extending from the *rotunda* Zone up to horizons well into the Portlandian. Casey's statement that the *albani* Zone fauna is the indigenous element in the Upper Lydite Bed (1967, p. 132) is not accepted. There is no doubt that the *albani* Zone fauna is present in that horizon as Casey has demonstrated (1967, p. 132), but there are later faunal elements present too. As stated earlier, in my opinion the holotype of *Lydistratites lyditicus* Buckman correlates with ammonites higher in the Portland Sand succession of Dorset than the *albani* Zone. This belief is confirmed by the fauna of the Glauconitic Beds above the Upper Lydite Bed, which requires correlation with horizons very high in the Dorset Portland Sand (Wimbledon and Cope 1978).

Russia (Volga Basin)

Correlation between the British Kimmeridgian/Portlandian succession and that of Russia has been the subject of controversy for many decades. The Russian Volgian faunas, characterized in their lower parts by the genera *Virgatites* and *Zaraiskites* have been sought in the uppermost Jurassic rocks of north-west Europe. Salfeld (1913) identified some of the British Upper Kimmeridgian forms with Russian species and introduced a zone of *Virgatites miatschkovensis* succeeded by a zone of *Perisphinctes pallasianus*. Neaverson later showed (1925) that the British forms were not related to the Russian faunas as Salfeld had supposed, and founded new genera for the British Upper Kimmeridgian ammonites.

Later discoveries of ammonites from the basal Portland Sand led Buckman to believe that he had found *Virgatites' scythicus* on the Dorset coast. These ammonites were later included in the genus *Progalbanites* Spath, 1936 (type species *P. albani* (Arkell, 1935)).

The relationship of *Progalbanites* to *Zaraiskites* has long been disputed. Arkell (1957) believed it to be synonymous with *Zaraiskites*, and recent correlations of the Dorset succession with the Volga Basin (e.g. Arkell 1956; Gerasimov and Mikhailov 1966) have relied on the identity of the *Zaraiskites* fauna with the *albani* Zone fauna of Dorset. Casey's demonstration of the fact that the *pallasioides* Zone fauna is older and not younger than the *rotunda* fauna, led him to re-examine these correlations (1967, pp. 131–133). His conclusion was that *Progalbanites* is younger than *Zaraiskites* and that in Britain *Progalbanites* occurs

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TEXT-FIG. 13. Suggested correlations between the upper part of the Upper Kimmeridgian and the type Volgian succession.

together with the Russian genus *Epivirgatites*, this latter genus having been previously described under various other names in Britain (Casey 1967, p. 132).

I intend to describe the ammonite faunas of the Portland Sand of Britain in the near future, but meanwhile I consider it useful to figure specimens here to show Dorset specimens of *Epivirgatites nikitini* (Michalski). Two specimens are figured in Pl. 55, figs. 2 and 3. The larger specimen shows the typical rib style of the species (and genus), in particular the constrictions preceded by a four-branched rib which is in effect a polygyrate rib with an extra secondary with a very low origin to the anterior of the primary rib. The association of this rib type with normal bifurcate ribs seems unique to *Epivirgatites*. The smaller figure shows the inner whorl development of the Dorset forms, and polygyrate ribs just as do specimens figured by Michalski (1894). These figured specimens were collected 1 m above the Portland Sand *Exogyra* Bed (Arkell 1947*a*, p. 120) at West Weare Cliffs on Portland Isle, a position at the top of the *albani* Zone.

Epivirgatites is entirely restricted to the *nikitini* Zone of the Volga Basin and the genus is therefore of paramount importance in the correlation of the two areas. Having thus established a firm point of correlation at the *albani* Zone horizon, one can look for possible points of correlation lower in the succession. The British *Dorsoplanites ultimus* (Neaverson) from the *pallasioides* Zone of the Midlands correlates with the

Dorsoplanites panderi Zone of the Volga Basin; the base of the *pavlovi* Subzone seems the most obvious level, as the *Dorsoplanites* specimens reputedly came from low in the Hartwell Clay (Neaverson 1925, p. 21) and in this way pavloviids of the *pallasioides* Zone can be taken as time-equivalents of clearly related species in the *pavlovi* Subzone. This suggests that the overlying *zarasjkensis* Subzone correlates with the British *rotunda* Zone, though there is no direct link between the two faunas. The *virgatus* Zone would then correlate with the *fittoni* and also probably lower *albani* Zones.

The next zone above the *nikitini* Zone in the Volgian succession is the *fulgens* Zone of the Upper Volgian, to be correlated as Casey (1967, p. 129) suggested with horizons younger than the Portland Stone. The Volgian stage must therefore be very incomplete and is clearly unsuitable as an international Standard Stage (Casey 1967, p. 132).

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Manuscript received 10 January 1975 Revised manuscript received 11 October 1977 JOHN C. W. COPE Department of Geology University College Swansea SA2 8PP